CHITINOZOAN ASSEMBLAGES FROM THE PRAGIAN (LOWER DEVONIAN) OF EASTERN AUSTRALIA

Theresa Winchester-Seeto

Centre for Ecostratigraphy and Palaeobiology, School of Earth Sciences, Macquarie University, New South Wales 2109

Winchester-Seeto, T., 1993:11:01. Chitinozoan assemblages from the Pragian (Lower Devonian) of eastern Australia. *Proceedings of the Royal Society of Victoria* 105 (2): 85–112. ISSN 0035-9211.

Two Pragian sections from seven eastern Australian successions investigated have yielded chitinozoans; they are the Martins Well Limestone Member of the Shield Creek Formation, north Queensland, and the Coopers Creek Formation at Boola Quarry, Victoria. Chitinozoa from these sections are documented and the new species *Gotlandochitina kutjala* and *Angochitina cactula* are described. Comparison of the assemblages recovered in this study with those of contemporaneous faunas from other areas of Australia (Garra Limestone), Europe and north Africa demonstrate the facility of chitinozoans for intercontinental correlation. *Angochitina comosa* Taugourdeau & Jekhowsky, a well-known early Pragian chitinozoan, was recovered from the Martins Well limestone, verifying the position of the Lochkovian–Pragian boundary as previously determined from conodont evidence, and establishing the importance of the species as a reliable index in Australia, as it is also in south-western and central Europe and north Africa. *Angochitina caeciliae* Paris and *Bulbochitina bulbosa* Paris occur in strata of similar age in Australia and south-western Europe. As in Europe, strata of late Pragian age in eastern Australia yield few chitinozoans, pointing to a world-wide trend of reduced chitinozoan diversity in this interval. Marine regressions and a reduced number of suitable environments for preservation of chitinozoans are possible reasons for this phenomenon. A number of diagnostic assemblages based on zone fossils from Europe can be recognised in Australian successions. These are an *Angochitina comosa* assemblage from near the Lochkovian–Pragian boundary, succeeded by an *Angochitina caeciliae* assemblage, still within the *sulcatus* conodont Biozone, and a *Bulbochitina bulbosa* assemblage from the *kindlei* conodont Biozone.

PRAGIAN chitinozoans have been studied from only a small number of localities, primarily from north Africa and south-western and central Europe, thus concentrating the data in a limited palaeogeographic range. Although chitinozoans have proven their utility as biostratigraphic tools in these areas, the lack of more widespread data has skewed our knowledge of this time interval, leaving a number of unanswered questions; these include doubts as to whether chitinozoan biozonations developed in Europe can be used in an Australian context, and the allied problem of how useful chitinozoans are for intercontinental correlation. Our knowledge is further restricted by the fact that there is only scanty information on the upper Pragian, most studies having examined material only from near the Lochkovian–Pragian boundary. The present investigation, in tandem with a recent study of chitinozoans across the Lochkovian–Pragian boundary in the Garra Limestone of central New South Wales (Winchester-Seeto 1993), seeks to address some of these issues.

The first studies of Early Devonian chitinozoans were concentrated in north Africa in re-sponse to the search for oil in the 1960s and 1970s. These studies included work on the Algerian Sahara (Taugourdeau & Jekhowsky 1960, Magloire 1967, Jardiné & Yapaudjan 1968), Libya (Massa & Moreau-Benoit 1976), Morocco (Rahmani 1978) and Tunisia (Grignani 1967). It is difficult to integrate this work fully with later investigations for two reasons. Firstly, these studies relied solely on illustrations from light microscopy, producing only silhouettes to document the fauna. It has since been demonstrated by Paris (1978, 1981a) that observations of opaque chitinozoans by light microscopy may omit important specific and generic characters, such as ornamentation, and may lead to misidentification of taxa (Paris 1978: 195). Consequently, comparisons between faunas illustrated solely as silhouettes and those depicted by scanning micrographs are unreliable. Secondly, the stratigraphic control on the original cores and sections used in these early studies may be based either on very limited information from other fossils or, in some cases, on outdated interpretations, thus requiring some revision. Paris (1981a: 357) attempted to

align the assemblages found by Taugourdeau & Jekhowsky (1960) and Magloire (1967) based on the chitinozoan zonation erected in France; this reinterpretation has been adopted in the present study.

Other studies on Pragian chitinozoans have included those from south-western Europe (France: Paris 1976, 1980, 1981a; Spain: Diez & Cramer 1978), central Europe (Poland: Wrona 1980; Bohemia: Chlupáč et al. 1985) and China (Gao 1986). The time parameters for the last study are not specific and only a pre-*dehiscens* age is given; the composition of the fauna, however, suggests a Pragian age. Paris (1981a) suggested amendments to the stratigraphic alignments for the Spanish study, and these have been adopted for the purposes of this investigation. The works of Diez & Cramer and of Gao use only silhouettes for identification, and thus their results must be treated with some caution.

The aims of the present study were:
1. To document chitinozoan faunas from the Pragian of eastern Australia.
2. To compare these faunal assemblages with studies of contemporaneous strata elsewhere in Australia and globally.
3. To evaluate the intercontinental utility of species used as index fossils in Europe.
4. To develop a preliminary zonation for eastern Australia.

METHODS

Seven sequences from eastern Australia, covering the entire Pragian interval, were investigated for this study (Figs 1, 2). The main criterion for selection of the limestone strata was that a firm biostratigraphic framework, based on conodont data, was already in place (e.g. Mawson et al. 1988, 1992; Wilson 1989). In order to achieve the greatest precision in correlating chitinozoan data with results obtained from conodont work, concurrent collections of conodont and chitinozoan samples were made from surface outcrops.

Methods of processing for chitinozoans followed those outlined by Paris (1981a), including initial treatment of 50 g of crushed rock with 10% HCl until all the carbonate had been dissolved, followed by acid digestion by 70% HF for 12–48 hours. Nitric acid (concentrated) was used when necessary for surface etching, dissolving of fluorite salts and destruction of amorphous organic matter. The residue was
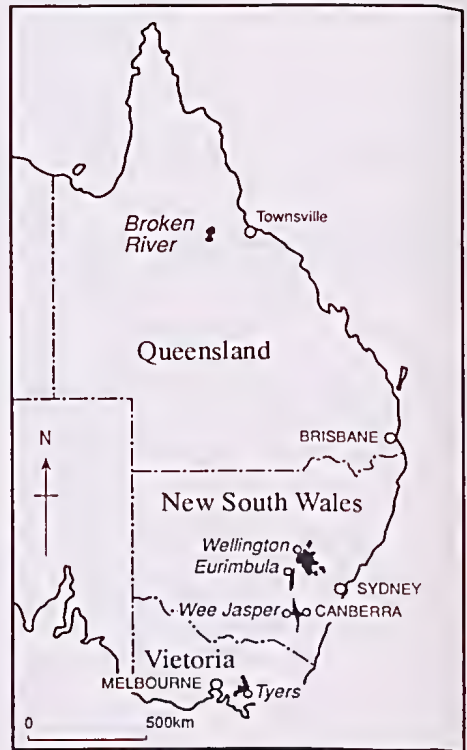

Fig. 1. Map of eastern Australia showing Lower Devonian strata investigated for this report.

then separated through a 53 μm sieve and picked with a micropipette. Representatives of each species, especially well-preserved specimens, were selected and mounted on glass coverslips for examination with a scanning electron microscope, as described by Paris (1981a).

SEQUENCES INVESTIGATED

Only two of the seven sequences investigated yielded well preserved chitinozoans in sufficient numbers to prove useful for such a biostratigraphic study. No chitinozoans were recovered from a section through the Garra Limestone near Eurimbla (EUR), central New South Wales, spanning the time interval from *delta* to *sulcatus* conodont Biozones (Sorentino 1989). A second section through the Garra Limestone near Mountain View homestead (MVR) yielded only three badly deteriorated, unrecognisable specimens; this section was documented by Wilson (1989) who suggested that the section probably included the *pireneae* conodont Biozone. A section through the Arch Creek Limestone

SYSTEM	STAGE	CONODONT ZONE	
LOWER DEVONIAN	EMSIAN	perbonus	
		dehiscens	
	PRAGIAN	pireneae	
		kindlei	
		sulcatus	
	LOCHKOVIAN	pesavis	
		delta	
		eurekaensis	
		woschmidti	

▓ Abundant chitinozoans
◩ Few chitinozoans
☐ No chitinozoans

Fig. 2. Stratigraphic ranges of Lower Devonian sequences investigated for this report. For detailed stratigraphic information see Mawson et al. (1988, 1992), Mawson & Talent (in press) and Wilson (1989).

member of the Shield Creek Formation, northern Queensland, spanning the *pesavis–sulcatus* conodont Biozones (Bear & Benson in Mawson et al. 1988) gave no results. The TANK section through the lower part of the Cunningham Formation (Talent & Mawson, in prep.), central New South Wales, and the CABL section of the Cavan Bluff Limestone at Wee Jasper, southern New South Wales (Mawson et al. 1992), covering the Pragian–Emsian boundary, were likewise barren of chitinozoans (see Figs 1, 2).

More promising results were obtained from a section through the Martins Well Limestone Member of the Shield Creek Formation in the Broken River area of northern Queensland. A small but nonetheless significant yield was also obtained from a measured section at Boola Quarry near Tyers, eastern Victoria.

The Martins Well Limestone Member has been thoroughly documented by Jell (1968), Telford (1975), Wyatt & Jell (1980) and, more recently, by Mawson et al. (1988). The limestone is a bioclastic calcarenite interpreted as representing a 'shallow marine deposition on a broad, stable shelf' (Wyatt & Jell 1980: 202), probably at the start of a marine transgression. The 120 m section (Fig. 3) measured through this limestone is the same as that sampled for the conodont work carried out by Benson & Bear (in Mawson et al. 1988) and repeats one of the studies by Telford (1975).
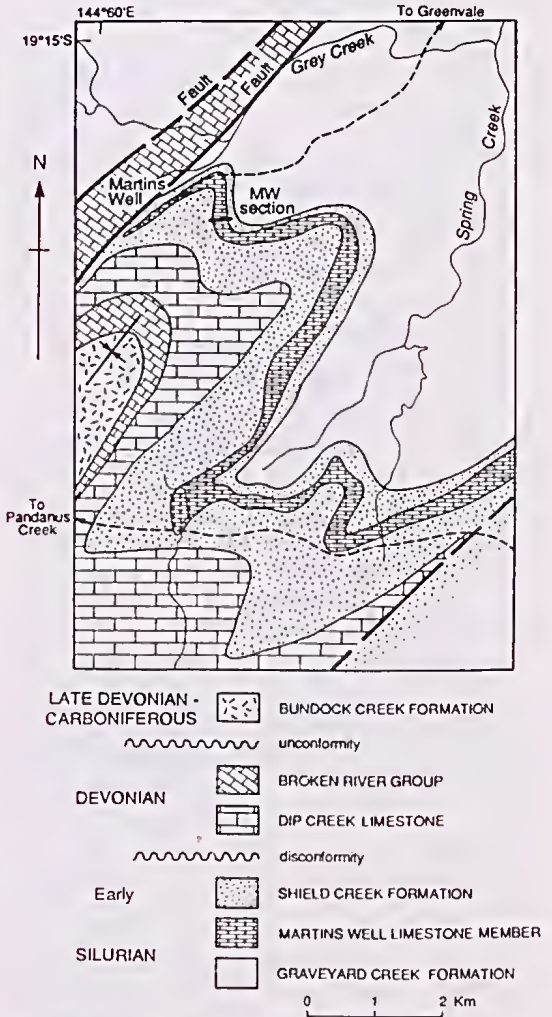

Fig. 3. The Broken River area of northern Queensland, showing the location of the Martins Well section (prefix MW); after Telford (1975).
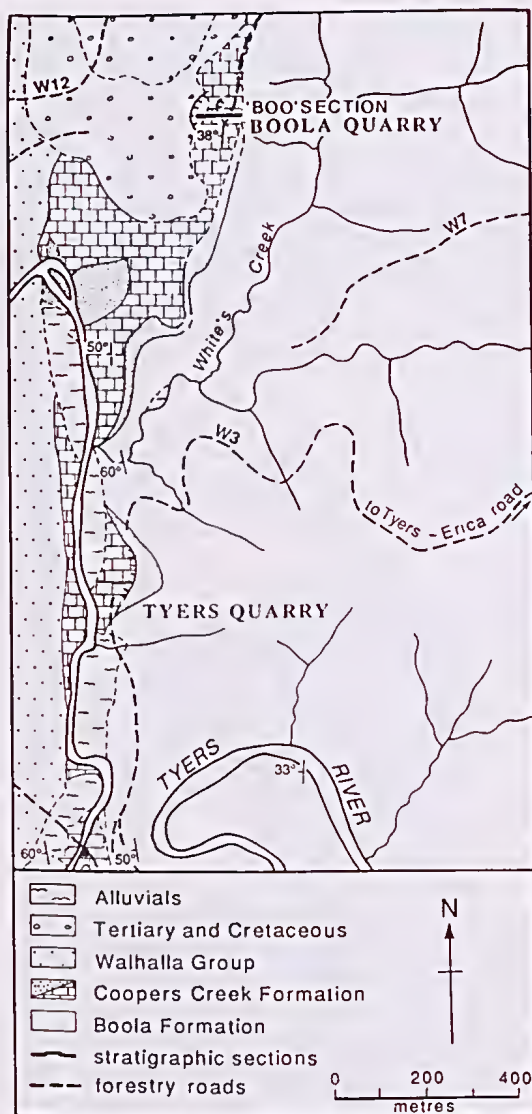
Fig. 4. The Coopers Creek Formation, showing the location of the section through Boola Quarry (prefix BOO); based on a map surveyed by Kenney (1937).

Boola Quarry is situated within the Tyers Limestone Member of the Coopers Creek Limestone. (Fig. 4). The limestone is generally richly fossiliferous, with faunas of corals and conodonts that were described by Philip (1962, 1965) and Philip & Pedder (1967). VandenBerg (1988: 122) suggested that the limestone represents a relatively shallow water deposit, with an unresolved question as to whether the strata are *in situ* or are the result of a mass-flow event.

Rehfisch & Webb (1993) reinterpreted the unit as a carbonate fan deposited in deep water, with possible reworking. The age of the strata has been unclear, but recent work by Mawson & Talent (in press) shows that, while the base of the Boola Quarry section is of *sulcatus* Biozone age, this zone is replaced low in the section by the *kindlei* Biozone, 7.1 m above the base of the Coopers Creek Limestone.

CHITINOZOAN DATA

Chitinozoan yields from the Martins Well Limestone are low to average, with fossils recovered in 18 out of 29 samples and ranging in abundance from 0.02 to 4 specimens per gram of limestone. The fauna is relatively well-preserved, amber to black in colour, with most individuals in full relief or only partially flattened. Breakages are common but some ornamentation is preserved on most specimens. Many chitinozoans display circular 'holes' resembling those figured by Laufeld (1974: 118) and which are interpreted as traces of parasites. These holes may have been partially responsible for the breakages by weakening the vesicle wall.

The chitinozoans from Martins Well tend to occur in beds either with no macrofossils or where these are only small in size. Small crinoid stems are commonly found in the same beds (e.g. bed numbers MW 13.7, 15.0, 18.6, 20.9, 25.4 rare, 34, 34.2, 39.9, 49.0, 51.0, 69, 74, 78.6, 95.6), but in some places crinoid calices, corals, bryozoans, small brachiopods, small gastropods and, more rarely, stromatoporoids occur together with the chitinozoans. The macrofossil assemblage suggests an extremely shallow depositional environment, and the presence of crinoid calices suggests a relatively quiet water regime. The microfauna consists of scolecodonts, conodonts and the linings of agglutinated microforaminiferans.

In contrast, Boola Quarry yielded very few chitinozoans or other microfauna, apart from conodonts which are relatively abundant. In the 20 m section in the lower part of Boola Quarry, commencing from the base of the Coopers Creek Limestone, only 4 beds out of 24 contained any trace of chitinozoans and only one bed produced more than 10 individuals. All chitinozoans recovered show a high degree of organic maturation; thin-walled genera are scarce, and those that do occur are represented by badly broken specimens with deteriorated surfaces having

little or no ornament. There are, however, some reasonably well-preserved specimens of thick-walled genera, e.g. *Bursachitina* and *Bulbochitina*, in full relief and with ornamentation more or less intact. The varied nature of the preservation suggests that conditions were not ideal for the conservation of these fossils and only robust groups were preserved. Few macrofossils were observed in the section and the microfauna is relatively sparse, consisting of rare scolecodonts and microforaminiferal linings, a few agglutinated foraminiferal tests and conodonts.

STRATIGRAPHIC DISTRIBUTION OF CHITINOZOA

Martins Well Limestone

The Martins Well fauna is dominated by four species, *Angochitina* sp. B, *Angochitina comosa* Taugourdeau & Jekhowsky, *Angochitina dimorpha* Taugourdeau & Jekhowsky and *Gotlandochitina kutjala* n. sp.; together these make up 53% of the population (Fig. 5; Table 1).

The results of the Martins Well study show a number of similarities with a previous investigation of a section through the Garra Limestone, spanning the Lochkovian–Pragian boundary (Winchester-Seeto 1993). Chitinozoans from the GCR (Golf Course) section of the Garra Limestone were assigned to three assemblages. Assemblage 1, from the top of the *pesavis* conodont Biozone, was characterised by the presence of *Angochitina hypenetes* Winchester-Seeto and also contained *Calpichitina gregaria*? Paris, *Muscochitina*? sp. and *Calpichitina velata* (Wrona). The succeeding Assemblage 2, located stratigraphically just above the Lochkovian–Pragian boundary (i.e. just into the *sulcatus* conodont Biozone), was defined by the occurrence of *Angochitina comosa* Taugourdeau & Jekhowsky and also included *Muscochitina*? sp. and *Calpichitina velata*. Assemblage 3, still within the *sulcatus* conodont Biozone, contained *Angochitina caeciliae* Paris, *Gotlandochitina* sp. C, *Bursachitina mawsonae* Winchester-Seeto, *Angochitina* aff. *A. crassispina* Eisenack, *Angochitina* cf. *A. callawayensis* Urban & Kline and *Gotlandochitina* aff. *G. ramosus* (Paris).

Five species from the Martins Well section were also found to occur in the lower Pragian segment of the GCR section: *Angochitina comosa*, *A. hypenetes*, *Bursachitina mawsonae*, *Angochitina* cf. *A. callawayensis* and *Ango-*

chitina aff. *A. crassispina*. The first three of these species occur in Assemblage 2 of the Garra Limestone. The presence of *A. comosa* very low in the section from the Martins Well Limestone indicates a close correlation with Assemblage 2 of the Garra Limestone, and thus a very early Pragian age (i.e. *sulcatus* conodont Biozone).

Benson & Bear (in Mawson et al. 1988) showed the base of the Martins Well Limestone to lie in the *pesavis* conodont Biozone, based on the occurrence of *Icriodus steinachensis* 8.5 m above the base of the section. They also suggested that the *pesavis* Biozone was represented much higher in the section by elements they refered to *Pedavis pesavis*? (Mawson et al. 1988, table 7). However, as these elements do not include an I element their assumption may be suspect. Further, the specimen they identified as *Kimognathus alexeii* has been re-examined and found to be a damaged specimen of a species of *Pedavis* (R. Mawson pers. comm.), casting doubt on the age of the upper part of the section. In his section No. 3658, parallel to the section from which Benson & Bear's samples were collected, Telford (1972, 1975) recovered two specimens of *Eognathodus sulcatus sulcatus* at 9 m and 10.5 m above the base of the section (Telford 1975, pl. 12, figs 5–7). With the incoming of *E. sulcatus* at this level it appears that the Lochkovian–Pragian boundary is fairly tightly constrained somewhere between 8.5 m and 9 m above the base of the Martins Well Limestone Member. This is corroborated by the presence of *Angochitina comosa* amongst the first yielding samples of the section used in the present study (i.e. sample MW 18.6, 24.6 m above the base of the section).

The absence of *Angochitina caeciliae* and *Gotlandochitina* aff. *G. ramosus* in the Martins Well material suggests that this section does not extend as high as Assemblage 3 of the Garra Limestone, despite the presence of *Angochitina* cf. *A. callawayensis* and *A.* aff. *A. crassispina* at Martins Well. Two species, previously known only from the Lochkovian in Australia, are now found to extend into the Pragian; i.e. *Gotlandochitina implicationis* (Urban) and *Angochitina* sp. A (formerly *Angochitina* sp. B of Winchester-Seeto 1993).

A number of key species also occur in faunas from overseas. *Angochitina comosa* has been found in the lower Pragian in north Africa (Taugourdeau & Jekhowsky 1960, Grignani 1967, Magloire 1967, Rahmani 1978), in Spain (Diez & Cramer 1978), in France (Paris 1976), in Bohemia (Chlupáč et al. 1985) and in China
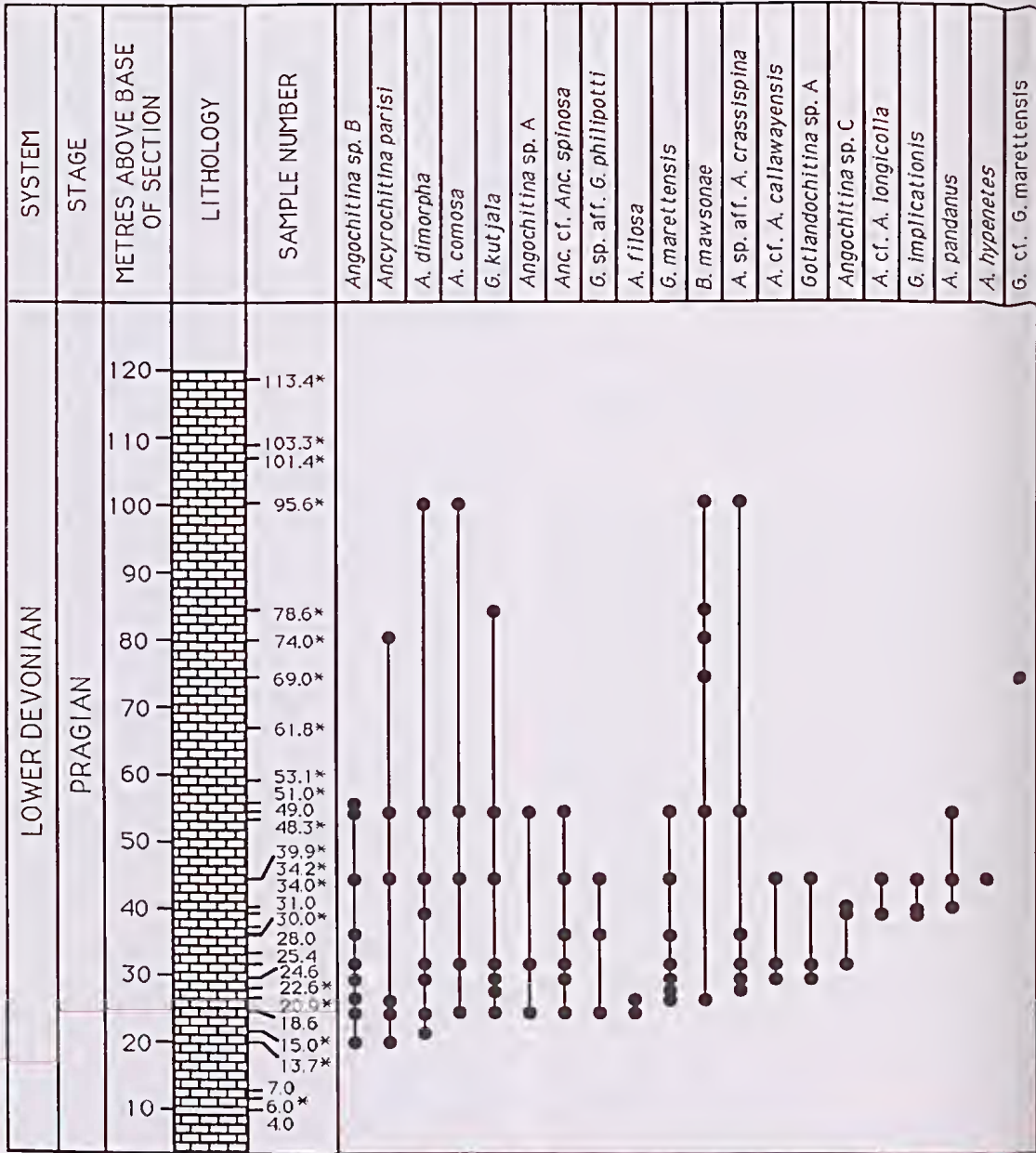
Fig. 5. Stratigraphic ranges of Chitinozoa in the Martins Well section (MW) of the Martins Well Limestone Member, Shield Creek Formation, Broken River area of northern Queensland; * indicates beds yielding conodonts.

(Gao 1986). Paris (1981a) used this species, along with *Margachitina catenaria tenuipes* Paris, to define his Zone 32, found just above the Lochkovian–Pragian boundary. *Angochitina dimorpha* was also found in the lower Pragian of north Africa (Taugourdeau & Jekhowsky 1960),

and *Angochitina cactula* n. sp. (= *Angochitina* cf. *A. crassispina* Eisenack of Wrona 1980) was found in the lower Pragian of Poland.

Slight differences exist in the stratigraphic position of some species. For instance, *Angochitina* cf. *A. callawayensis* was found slightly

Sample Number	MW 13.7	15	18.6	20.9	22.6	24.6	25.4	30	34	34.2	39.9	49	51	69	74	78.6	95.6	BOO 13.1	17.8	28
Meters above base of section	19.7	21	24.6	26.9	28.6	30	31.4	36	40	40.2	45.9	55	57	75	80	84.6	102	13.1	17.8	28
Anc. sp. aff. A. parisi	1										2	2								1
Angochitina sp. B	1		17	1		18	21	2			18	11								
A. dimorpha		1	28			12	34				13	5			1					
A. comosa			20				43				3	4	1				1			
Angochitina			22				2					2					2			
G. sp. aff. G. philpotti			3					2			8									
G. kulala			12			24	31		1		24	9				1				
Anc. spinosa var. gibba			31		1	5	8	1			2	1								
G. marettensis				1		11	15	2			21	3		1		2	3			
B. mawsonae				1				1									1			
A. sp. aff. A. crassispina				2		7	4				2	3		1		2				
Gotlandochitina										8		3								
A. cf. A. callawayensis						6	1			5	12									
Angochitina sp. C						5	6			2										
Angochitina sp. E							26													
G. implications				2					4		2				1					
A. cactula						2		2	2		1									
A. hypenetes											1	1								
G. cf. G. marettensis												13								
Sp. indet			17			7	10	2		4	13	3								
B. bulbosa																		22	3	
Bursachitina												8					2	5	2	
Gotlandochitina																				

Table 1. Distribution and abundance of chitinozoans from the Martins Well section (MW) of the Martins Well Limestone Member, Shield Creek Formation, and from the Boola section (BOO) of the Tyers Limestone Member, Coopers Creek Formation.

higher stratigraphically by Paris (1976) in Saint-Céneré. *Ancyrochitina spinosa gibba* n. var. has previously been cited only from the Middle Devonian (Urban & Kline 1970), but this taxon appears to be merely a morphological variant of *A. spinosa* Eisenack, which ranges from the Silurian to the Middle Devonian. Similarly, *Gotlandochitina marettensis* Paris has only previously

been found in the Emsian (Paris 1981a, 1981b), though there is a possible evolutionary relationship between this species and *Angochitina bifurcata* Collinson & Schwalb, found in the Lochkovian. This would account for its presence in the Pragian of Australia.

Several important species, common in coeval deposits across the world, are missing from Australian strata so far studied: *Fungochitina pistilliformis lata* (Taugourdeau & Jekhowsky), *Angochitina devonica* Eisenack and *Cingulochitina serrata* Taugourdeau & Jekhowsky from south-western Europe and north Africa; *Urochitina simplex* Taugourdeau & Jekhowsky from north Africa; *Armoricochitina ceneratiensis* (Paris) from south-western Europe; *Margachitina caternaria tenuipes* Paris from south-western and central Europe as well as north Africa; and *Ancyrochitina ancyrea* (Eisenack) and *Ancyrochitina tomentosa* Taugourdeau & Jekhowsky from central Europe and north Africa. The reasons for the absence of these species in Australia is unknown, but it is interesting to note that four of the genera—*Urochitina, Cingulochitina, Armoricochitina* and *Margachitina*—have not yet been found in any Australian deposit, nor were they reported in the Chinese fauna documented by Gao (1986).

Boola Quarry

Only four species were recovered from the section at Boola Quarry: *Bulbochitina bulbosa* Paris, *Gotlandochitina* sp. B, *Bursachitina* sp. and *Angochitina* sp. D (Table 1). *Gotlandochitina* sp. B was also found in Assemblage 3 of the Garra Limestone; this assemblage occurred directly above that containing *Angochitina comosa*.

Bulbochitina bulbosa was used by Paris (1981a: 379) to define his Zone 36 for south-western Europe; this zone occurs in the middle Pragian, within the *kindlei* conodont Biozone. *B. bulbosa* occurs only in two samples from Boola Quarry: sample BOO 13.1, approximately 6 m above the *sulcatus–kindlei* boundary which is 7.1 m above the base of the section (Mawson & Talent in press); and sample BOO 17.8, 11 m above the boundary. The occurrence of *B. bulbosa* in Australia is thus stratigraphically very close to but slightly lower than its occurrence in Europe.

PROBLEMS IN THE PRAGIAN

Chitinozoans have been recovered from Pragian strata in only three sections in Australia, two

from near the boundary of the *pesavis–sulcatus* conodont biozones and one spanning the *sulcatus–kindlei* boundary. Despite repeated attempts in a number of other Pragian limestone successions (representing a range of different environments) no other strata yielded chitinozoans. Approximately 100 samples from six sections spanning the *kindlei* and *pireneae* conodont biozones in eastern Australia were processed for chitinozoans; only seven of these samples yielded chitinozoans and only four produced specimens that were well enough preserved to identify, the latter being from Boola Quarry (Winchester-Seeto unpub. data).

This stratigraphic interval, covering the upper *sulcatus* to the lowermost *dehiscens* conodont biozones (i.e. middle Pragian to just above the Pragian–Emsian boundary), is documented in only four studies world-wide (Paris 1981a, 1981b; Massa & Moreau-Benoit 1976; Diez & Cramer 1978). The small number of investigations may indicate a lack of interest in this interval or reflect unsuccessful attempts to find chitinozoans. The latter is certainly true for Australia, as exemplified by the difficulties encountered in finding suitable localities where chitinozoans can be recovered. Unpublished studies from Europe and north Africa suggest, however, that at least in the northern hemisphere the problem may be related to insufficient exploration (Paris pers. comm. 1992).

Where chitinozoans have been recovered from the middle and upper Pragian, it is apparent that their abundance in this interval is much lower than in other parts of the Lower Devonian and that species diversity is also reduced. Similar patterns have been observed by some researchers on conodonts; for example, Sweet (1985: 490) presented a graph showing that the species diversity of conodonts from the Upper Cambrian to the top of the Lower Devonian reaches a peak near the Lochkovian–Pragian boundary and drops dramatically to a low near the middle of the Pragian, before rising slightly at the Pragian–Emsian boundary. Bayer & McGhee (1989: 7) presented a similar plot, with a decrease in species diversity appearing slightly higher in the Pragian (Siegenian) and continuing well into the Emsian (the differences in timing of these events may be an artefact of the sampling and graphical procedures used by the different workers). Other researchers found that the drop in conodont species diversity occurs much lower stratigraphically and thus precedes that shown by chitinozoans. Ziegler & Lane (1987: 153) noted a decrease in conodont species diversity in the uppermost *pesavis* conodont Biozone, followed by a prolonged interval of low diversity until very high in the Pragian. Data from the Garra Limestone also showed a drop in conodont species diversity high in the upper Lochkovian *pesavis* Biozone (Talent et al. in press).

Although the exact timing is difficult to assess, given the data available, there appears to be a widespread or global event occurring in the Pragian, affecting both conodonts and chitinozoans (and perhaps other microfauna and macrofauna). The reason for such a drop in diversity is unclear, but in the *kindlei–pireneae* interval (when chitinozoan abundance and diversity is lowest) a marine regression has been postulated for Australia (Talent & Yolkin 1987).

As a number of chitinozoan species (e.g. *Angochitina dimorpha* Taugourdeau & Jekhowsky, *Ancyrochitina parisi* Volkheimer, Melendi & Salas and *Sphaerochitina nodulosa hispida* Taugourdeau & Jekhowsky) occur before and after but not within this interval, an extinction event is not indicated. Added to this is the observation that genera with thin-walled vesicles (such as *Angochitina* or *Gotlandochitina*) are under-represented in the middle and upper Pragian, or are frequently so poorly preserved as to be unidentifiable at the species level (e.g. Boola Quarry, this study; Paris 1981a: 342). Recently, Paris (pers. comm. 1992) recovered representatives of thin-walled forms from well-preserved material from north Africa, but this limited occurrence underlines the comparative rarity of pristine preservation conditions in this stratigraphic interval.

These observations suggest that the drop in species diversity may be connected with preservation of the fossils, rather than a real gap in their temporal distribution. It has long been believed that chitinozoan vesicles do not survive in highly oxidised environments because the organic test is rapidly decomposed (e.g. Laufeld 1974, Paris 1981a). Perhaps the reduced number of chitinozoans in this stratigraphic interval can be explained by a decrease in the number of environments suitable for the preservation of the fauna, i.e. dysaerobic environments. Our understanding of the causes of low oxygen environments is limited and includes models ranging from stratified basins, based on salinity or thermal differences, upwelling, expansion or contraction of the oxygen minimum zone, and the effect of sea level and/or bottom topography (Tyson & Pearson 1991). A change in any one of these factors, or perhaps a combination of them,

may have led to a reduction in suitable preservation sites for organic microfossils.

More work is needed to establish whether the paucity of data for this interval represents a real gap in the geographic and/or temporal distribution of chitinozoans or is an artefact of sampling. Further study is also required to verify the apparent decrease in numbers of thin-walled genera.

PRELIMINARY CHITINOZOAN BIOZONATION FOR EASTERN AUSTRALIA

The only recent attempt to erect a chitinozoan biozonation for the Devonian was by Paris (1981a) for south-western Europe. There are a number of similarities between the assemblages found there and in Australia, and a number of

SYSTEM	STAGE	CONODONT ZONE	CHITINOZOAN BIOZONES OF AUSTRALIA (PRELIMINARY)	CHITINOZOAN BIOZONES OF S.W. EUROPE (PARIS, 1980)
LOWER DEVONIAN	EMSIAN	dehiscens		Burs. riclonensis/ Bulb. bulbosa 37
				36
		pirenae	/////	Bulb. bulbosa
			NO YIELDS AT THIS TIME	
	PRAGIAN	kindlei	/////	35
				Burs. maritima
		sulcatus	Bulb. bulbosa ?— — — — — ? ?— — — —?—	
			A. caeciliae	34 G. jouannensis/ A. caeciliae
			A. comosa	33 M. catenaria tenuipes A. comosa/ 32 M. catenaria tenuipes

Fig. 6. Preliminary chitinozoan biozonation of the lower Pragian in eastern Australia, and a comparison with the biozonation erected by Paris (1981a) for south-western Europe.

differences (Fig. 6). Zones 31 and 32 from Europe are partially based on the presence of *Margachitina catenaria tenuipes* Paris; however, *Margachitina* has not yet been found in Australia and is thus unavailable for stratigraphic use here. Zone 31 also contains *Angochitina comosa* Taugourdeau & Jekhowsky, found in a similar position (i.e. close to but slightly above the Lochkovian–Pragian boundary) in both the Garra Limestone and the Martins Well Limestone. In Australia, *A. comosa* is usually accompanied by *A. hypenetes* Winchester-Seeto and *Bursachitina mawsonae* Winchester-Seeto. Thus the first diagnostic assemblage in Australia is characterised by the first occurrence of *A. comosa*.

Work on the Garra Limestone demonstrated that the assemblage containing *A. comosa* was immediately followed by one containing *Angochitina caeciliae* Paris (Winchester-Seeto 1993). In Europe, Zones 31 and 32 are followed by a zone containing both *A. caeciliae* and *Gotlandochitina jouannensis* Paris; the latter has not yet been found in Australia. Based only on the Garra Limestone, so far, the next Australian assemblage could be defined by the first appearance of *A. caeciliae*. In the Garra Limestone this species was accompanied by *A. comosa, B. mawsonae* and *Gotlandochitina* cf. *G. ramosus* Paris.

Bursachitina maritima (Paris), used by Paris to define Zone 34 from Europe, has yet to be found in Australia. On the other hand, *Bulbochitina bulbosa* Paris, from Zone 36 near the top of the Pragian, has been found in Australia from the *kindlei* conodont Biozone.

Thus, based on the limited data from the three areas studied to date, it has been possible to recognise three distinctive and diagnostic assemblages from Pragian strata in Australia. That intracontinental correlation is possible is exemplified by the presence of *Angochitina comosa* in the GCR section of the Garra Limestone and in the Martins Well section, the entry of the species in both sections being approximately contemporaneous according to conodont data. The same three assemblages, moreover, enable intercontinental correlation. *A. comosa*, for example, has been used in conjunction with the conodont *Eognathodus sulcatus sulcatus* Philip for definition of the Lochkovian–Pragian boundary at the global stratotype in Bohemia (Chlupáč & Oliver 1989) and can be used similarly in Australian strata. The *Angochitina caeciliae* assemblage occurs stratigraphically above *A. comosa* in south-western Europe, within the *sulcatus* conodont Biozone, as it does in Aus-

tralia, but without the intervening *Margachitina catenaria tennipes* assemblage. *Bulbochitina bulbosa* is found within the *kindlei* conodont Biozone in Australia and in south-western Europe. Despite the slight anomalies between occurrences in Europe and Australia, the wide geographic spread and short stratigraphic time-span of the assemblages listed above make them useful additions to the biostratigraphic arsenal of Australian palaeontologists (see Fig. 6).

CONCLUSIONS

1. Chitinozoans have proved to be of biostratigraphic value in the lower Pragian of eastern Australia; diagnostic assemblages based on zone fossils from Europe can be recognised in Australian strata, facilitating subdivision of the *sulcatus* conodont Biozone.

2. The middle and upper Pragian of eastern Australia seems to be lacking deposits that yield abundant, well-preserved chitinozoans. This may be a worldwide phenomenon.

3. Three species in particular prove to have intercontinental utility in correlation, namely *Angochitina comosa* Taugourdeau & Jekhowsky, *A. caeciliae* Paris and *Bulbochitina bulbosa* Paris. Other species that may also be useful are *Angochitina dimorpha* Taugourdeau & Jekhowsky, *A. cactula* n. sp., *Ancyrochitina spinosa gibba* n. var. and *Gotlandochitina implicationis* (Urban).

4. Four genera (*Urochitina, Cingulochitina, Armoricochitina* and *Margachitina*) have so far not been recovered in Australia, suggesting that their distribution may be provincial or perhaps facies dependent.

SYSTEMATIC PALAEONTOLOGY

As there is no universally accepted suprageneric nomenclature for chitinozoans, the system used by Laufeld (1974) has been followed with the genera listed alphabetically. Abbreviations used for genera are: *Anc.* = *Ancyrochitina, A.* = *Angochitina, Bu.* = *Bulbochitina, B.* = *Bursachitina, G.* = *Gotlandochitina.*

All measurements are taken in microns (μm). Abbreviations used in the text are: L = length of vesicle; Lc = length of chamber; Ln = length of neck; Dmax = maximum diameter of chamber; Dn = diameter of neck; Da = diameter of aperture; Lsp = length of spines.

A correction factor of 0.7 has been used for those individuals whose diameter has been dis-

torted by total flattening; this follows, in part, the precedent set by Jaglin (1986). Most of the specimens recovered in this study were in full relief or only partially flattened, so that this correction was applied infrequently.

Type and figured specimens are housed in the collections of the Queensland Museum, South Brisbane (numbers prefixed by QMF) and the Museum of Victoria, Melbourne (numbers prefixed by NMV P). Localities are designated as MW for samples from the section through the Martins Well Limestone and BOO for the section in Boola Quarry.

Morphological terms used in this paper are those defined by Laufeld (1974: 37–38) and by Paris (1981a: figs 56, 57).

Genus Aneyrochitina Eisenack, 1955

Type species. Conochitina ancyrea Eisenack, 1931.

Aneyrochitina aff. Ane. parisi Volkheimer, Melendi & Salas, 1986

Fig. 7F–I

Material. Twenty-four specimens from samples MW 18.6 and 49.

Measurements. Taken from six specimens from samples MW 18.6 and 49. L 146–172 (Av. 157.3); Lc 78–99 (Av. 89.5); Ln 54–81.6 (Av. 67.6); Dmax 54.4–64.3 (Av. 59.8); Dn 20.2–34 (Av. 27.2); Lsp max 13.6; L/Lc 1.6–2.0; L/Dmax 2.3–2.9.

Description. A species of *Ancyrochitina* with a cylindrical neck surmounting an ovoid to conical chamber. Flexure is indistinct, leading to a relatively long neck occupying one-third to one-half the total vesicle length. The base is convex but may be flat to weakly concave in compressed specimens.

Surface sculpture appears at the basal edge or on the neck, with occasional spine bases visible on the flanks. Basal processes are generally short and may be simple or bifurcate, in some instances with the distal ends joined. Ornamentation on the neck consists of relatively short, simple spines which spread up to the oral periphery.

Remarks. The specimens from Martins Well closely resemble *Ancyrochitina parisi* from Argentina but include some individuals with a more ovate chamber with maximum diameter about half-way along the length of the chamber, in addition to the more typical conical chamber shape of *Anc. parisi.* The Australian specimens are approximately half the size of those from Argentina, but the proportions of total length to
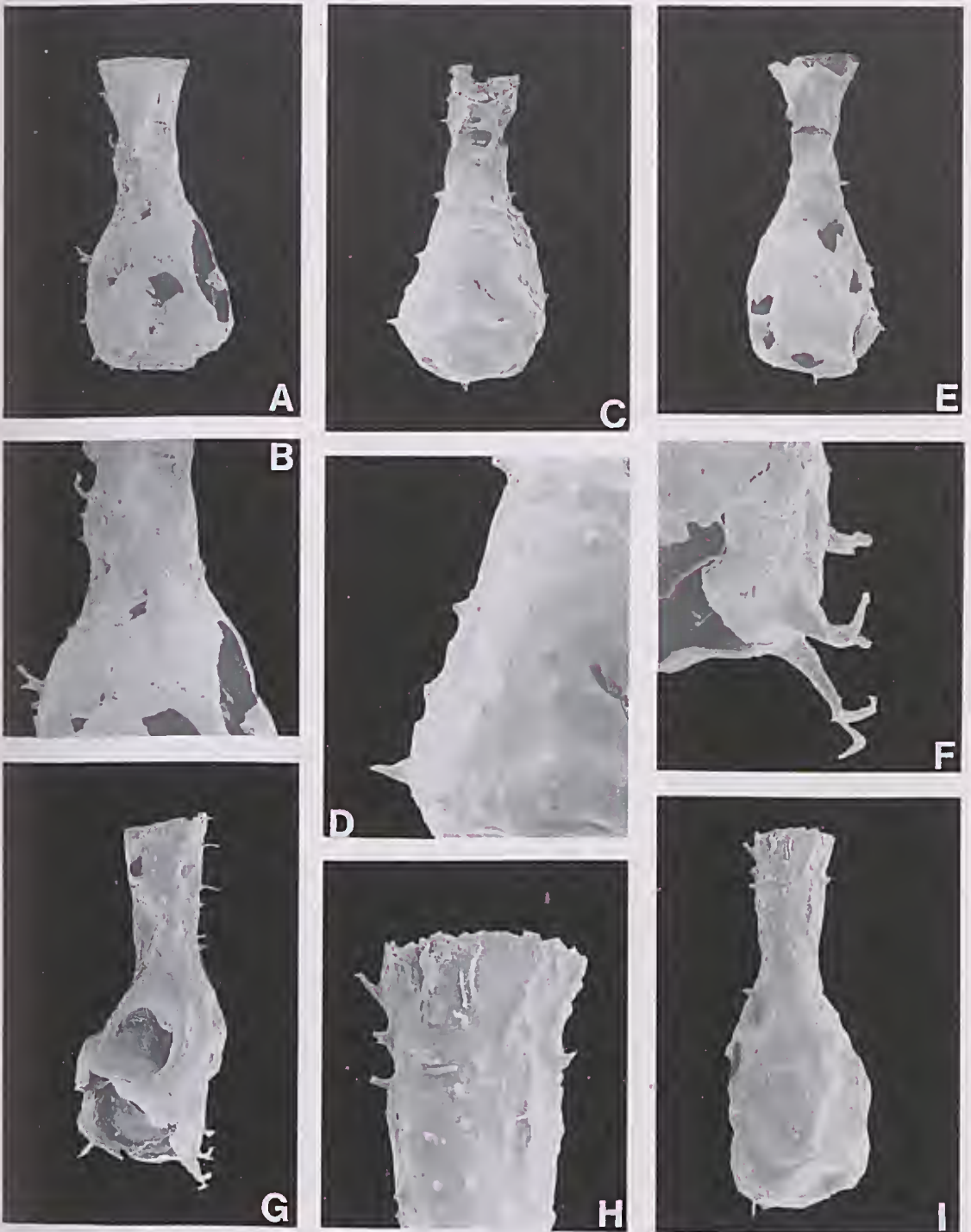
Fig. 7. A–E, *Angochitina* sp. B. A, B, QMF 25482, × 300, and enlargement of neck × 600, MW 39.9. C, D, QMF 25483, × 350, and enlargement of chamber showing unusual ornamentation × 900, MW 24.6. E, QMF 25484, × 350, MW 24.6. F–I, *Ancyrochitina* aff. *Anc. parisi* Volkheimer et al., MW 49. F, G, QMF 25485, enlargement of base of chamber showing appendices × 1300, and × 350. H, I, QMF 25486, enlargement of neck × 1000, and × 350.

length of body chamber, total length to maximum diameter, and length of ornamentation to total length are similar.

Sculptural elements are also very similar but in general, as is often the case in Australian material, they are much shorter; for example, *Anc.* aff. *Anc. parisi* has shorter basal processes and shorter spinose ornamentation on the neck. Basal processes are also much finer on *Anc.* aff. *Anc. parisi*. Rare examples can be found of specimens with distal processes joined by a membrane, both on the neck and on the basal edge; this parallels the occurrence noted by Volkheimer et al. (1986).

Additional, better preserved material of the Australian taxon may show it to be conspecific with *Anc. parisi*.

Ancyrochitina spinosa var. gibba n. var.

Fig. 8H

Ancyrochitina spinosa Eisenack 1959: 13–14, pl. 2, figs 1–2.
Ancyrochitina cf. *Anc. spinosa*.—Urban & Kline 1970: 71, pl. 18, figs 1–3, 14.

Etymology. Latin 'gibber' meaning swollen, referring to the shape of the neck.

Holotype. Urban & Kline (1970, pl. 18, fig. 1).

Type locality. Cedar City Formation, Whetstone Creek, north of Williamsburg, Missouri.

Paratype. Urban & Kline (1970, pl. 18, fig. 3).

Material. Eighteen specimens from samples MW 25.4 and 39.9. The specimens are broken and the ornamentation is greatly eroded.

Measurements. Taken from four specimens from samples MW 25.4 and 39.9. L 117–156.4 (Av. 131.9); Le 75–109 (Av. 88); Ln 42–48 (Av. 43.9); Dmax 67–84 (Av. 72.8); Dn 25.5–30 (Av. 27.4); Lsp 3.2–4.5 (Av. 3.9); Ln/L 0.3–0.35; L/Dmax 2.2–2.7.

Diagnosis. Shape same as *Ancyrochitina spinosa* (s.s.); neck cylindrical at base, swelling near middle and expanding slightly at aperture.

Description. A variety of *Ancyrochitina spinosa* with a conical to elongate club-shaped chamber, with a gentle but definite flexure. The chamber narrows considerably to a relatively short, cylindro-conical neck. The main feature of this new variety is the presence of a swelling near the middle of the neck; the base of the neck is a narrow cylinder but this expands slightly, giving an inflated appearance around what may be the prosome. After this 'bump' the neck continues either as a broad tube or as a cone. A fringed, slightly flared collar encircles the aperture. The chamber base varies from flat to convex, with a well rounded basal edge.

A relatively dense covering of spines is randomly distributed over the vesicle surface. These spines may be simple, bifurcate or multifurcate, some with broad bases. Smaller, finer spines may be observed on the neck.

Remarks. Due to the generally poor preservation of specimens from Martins Well, the holotype for this new variety has been chosen from the first specimens described with the unusual form of the neck (Urban & Kline 1970). This feature is quite obvious in some individuals but flattening of the neck may obscure its presence in others. Although a minor difference, the neck swelling appears to be a consistent feature within the populations where it is found. At this stage no stratigraphic significance is attributed to its distribution.

This new variety can also be distinguished by its slightly shorter neck; e.g. Ln/L = 0.3–0.35 from Martins Well, 0.35–0.38 from the Cedar City Formation (measured from Urban & Kline 1970, pl. 18, figs 1–2), 0.42–0.43 from the Baltic (measured from Eisenack 1959, pl. 2, figs 1–2), whereas Dunn (1959) reported a range of 0.4–0.47. Shorter, finer spines on the neck also differentiate this variety from typical members of the species.

Poor preservation of ornamentation on the Martins Well specimens makes it impossible to demonstrate the existence of 'antler-like' spines mentioned by Eisenack (1932) and Urban & Kline (1970). The Martins Well material has generally shorter spines than those depicted by Urban & Kline (1970) and Eisenack (1959), but Eisenack (1964) noted that specimens with reduced spines made up some of the population of *Anc. spinosa* and the same degree of intraspecific variation may apply here.

Anc. spinosa appears to have a very long stratigraphic range, from the Silurian to the Middle Devonian. This is paralleled by the occurrence of this new variety.

Fig. 8. A–E, *Gotlandochitina kutjala* n. sp., MW 18.6. A, D, holotype QMF 25492, × 300, and enlargement of chamber wall showing spine form and density × 900. B, C, paratype QMF 25493, ×300, and enlargement of chamber wall and ornamentation × 1300. E, paratype QMF 25494, × 300. F, G, *Gotlandochitina* sp. A, QMF 25495, × 400, and enlargement of broken chamber wall displaying ornamentation × 1000, MW 39.9. H, *Ancyrochitina spinosa* var. *gibba* n. var., broken specimen QMF 25496, × 350, MW 24.6. I, *Bursachitina mawsonae* Winchester-Secto, QMF25497, × 300, MW 49.

Genus Angochitina Eisenack, 1931

Type species. Angochitina echinata Eisenack, 1931.

Angochitina cactula n. sp.

Fig. 9A–E

? *Angochitina* cf. *A. crassispina* Eisenack.—Wrona 1980: 129, pl. 27, figs 1–6.

Etymology. A diminutive of 'cactus', from the Latin for a prickly plant, referring to the form of the spines.

Holotype. QMF 25476, Fig. 9A.

Type horizon and locality. MW 49, 55m above the base of the MW section of the Martins Well Limestone, Shield Creek Formation, Broken River area of north Queensland.

Paratypes. QMF 25477, Fig. 9B–C; QMF 25478, Fig. 9D–E.

Other material. Thirteen specimens from samples MW 34.2, 39.9 and 49.

Measurements. Taken from ten specimens from samples MW 34.2, 39.9 and 49. L 141–166.5 (Av. 152); Lc 85–107 (Av. 91.6); Ln 55–74.6 (Av. 63); Dmax 44–73 (Av. 60.6); Dn 26–38 (Av. 28.8); Lsp 3–25 (Av. 12.1); Ln/L 0.4–0.46; L/Dmax 2.1–2.9.

Diagnosis. Chamber subcylindrical to elongate elliptical; neck subcylindrical to conical; strong, thorn-like spines sparsely distributed over vesicle surface.

Description. The chamber shape varies considerably; though most commonly an elongate ellipse, flattening or partial flattening may produce a conical to almost rectangular form. This distortion may also affect the base, giving a convex, chevron or even flat aspect. Flexure is very elongate, and the position of the base of the neck is often difficult to determine. The subcylindrical to conical neck occupies less than half the total vesicle length and is topped with a conspicuous, fringed collar.

Ornamentation consists of a sparse covering of strong, broad-based, thorn-like spines that are mostly simple, but rare bifurcate spines can be observed. Some spines are curved towards the aperture. The spines and broken spine bases appear to be randomly distributed over the vesicle surface, with little evidence of a linear arrangement. The spines occur predominantly on the chamber, base and lower neck; those on the upper neck are reduced in length and thickness.

Remarks. In spine form and distribution, *A. cactula* is strikingly similar to *A.* cf. *A. crassispina* depicted by Wrona (1980). The only difference lies in the larger size of the Polish species and in its slightly longer neck; as this is considered to have no taxonomic significance, Wrona's form has been tentatively placed in *A. cactula.*

A. crassispina Eisenack shows a number of similarities to *A. cactula,* especially in vesicle shape. Differences in ornamentation, including a greater number of spines, a concentration of spines on the lower part of the neck and a paucity of lambda-shaped spines, serve to differentiate *A. cactula.*

Eisenack (1964) discussed the close relationship between *A. crassispina, A. echinata* Eisenack, *A. filosa* Eisenack and other species, placing them together with intermediate forms in a 'Formengruppe'. *A. cactula* shows a number of similarities with this 'Formengruppe'. Intraspecific variation in chamber shape and spine density of all the groups makes species assignment difficult, especially when based on a small number of specimens. This is further hampered by the problem that Eisenack's photographs are only silhouettes, making comparisons of ornamentation very difficult. Despite the resemblance of the Queensland specimens to *A. filosa* as depicted by Eisenack (1968) and Wrona (1980), they are assigned to a new species because of the presence of predominantly broad-based spines, the greater number of neck spines and the comparatively short neck.

Angochitina cf. A. callawayensis Urban & Kline, 1970

Fig. 10D, E

Angochitina cf. *A. callawayensis.*—Paris 1976: 95, pl. 19, fig. 9, pl. 26, fig. 5.—Winchester-Seeto 1993: fig. 6.8–6.9.

Material. Twenty-three specimens from samples MW 24.6 and 39.9.

Measurements. Taken from five specimens from samples MW 24.6 and 39.9. L 119–150 (Av. 133.5); Lc

Fig. 9. A–E, *Angochitina cactula* n. sp., MW 49. A, holotype QMF 25476, × 350. B, C, paratype QMF 25477, × 300, and enlargement of neck × 600. D, E, paratype QMF 25478, × 300, and enlargement of neck × 900. F, *Angochitina* sp. A, QMF 25479, × 350, MW 18.6. G, H, *Angochitina* aff. *A. crassispina* Eisenack, QMF 25480, × 350, and enlargement of vesicle wall × 1500, MW 24.6. 1, *Angochitina* sp. E, QMF 25481, × 300, MW 39.9.

84–93 (Av. 87.6); Ln 38–57 (Av. 46.2); Dmax 52–60 (Av. 55.6); Dn 24–32 (Av. 27.8); Lsp 5–7.5 (Av. 6.6); Ln/L 0.24–0.38; L/Dmax 2.3–2.6.

Remarks. The silhouette and the presence of fine, wispy, bizarre-shaped spines is strongly reminiscent of *A.* cf. *A. callawayensis* from the Garra Limestone (Winchester-Seeto 1993). Specimens from Martins Well have shorter spines but this may reflect the poor preservation. Both the Garra specimens and those from Martins Well have more slender, ovoid vesicles than those figured by Paris (1976).

No alignment of spines is observed on individuals from Martins Well. Many spines display very fine distal terminations; several on each specimen are bent, forked or T-shaped close to the tip of the spine, a characteristic feature of this species in both the Garra Limestone and Martins Well sections.

Angochitina comosa Taugourdeau & Jekhowsky, 1960

Fig. 10A, B

Angochitina comosa Taugourdeau & Jekhowsky 1960: 1221, pl. 3, figs 33–35.—Grignani 1967: pl. 1, fig. 18.—Magloire 1967: pl. 3, fig. 18.—Diez & Cramer 1978: 207, pl. 1, fig. 16.—Rahmani 1978: 278, pl. 2, figs 7, 8.—Paris in Chlupáč et al. 1985: pl. 3, fig. 13.—Winchester-Seeto 1993: fig. 6.13–6.15.
Angochitina cf. *A. comosa.*—Paris 1976: 95, pl. 19, figs 1, 2.
? *Angochitina echinata.*—Eisenack 1972a: 71, pl. 17, figs 1–14.

Material. Seventy-five specimens from samples MW 18.6, 20.9, 25.4, 39.9 and 95.6.

Measurements. Taken from fifteen specimens from samples MW 18.6, 20.9, 25.4, 39.9 and 95.6. L 114.7–159.1 (Av. 140.4); Lc 75–100.8 (Av. 87); Ln 29.6–78.2 (53.5); Dmax 47.6–69.6 (Av. 60.9); Dn 21–37.4 (Av. 32.6); Lsp 3.4–7.2 (Av. 5.3); L/Dmax 1.9–2.7; L/Ln 2.5–2.9.

Remarks. The specimens from Martins Well resemble those from the Garra Limestone in New South Wales (Winchester-Seeto 1993) and fall readily into the range of dimensions determined for the Garra specimens. Small differences in ornamentation on the Martins Well specimens include a slightly lower spine density (4–6 per 100 μm²) and rare bifurcate spines scattered amongst the simple ones, thus contrasting with the New South Wales material in which bifurcate spines are more common. The individual spines also appear to be thicker than those from the Garra Limestone but this may reflect preservation and the organic 'glue' that covers many specimens.

Angochitina aff. A. crassispina Eisenack, 1964

Fig. 9G, H

Angochitina aff. *crassispina* Eisenack.—Winchester-Seeto 1993: fig. 7.8.

Material. Fifteen specimens from samples MW 22.6, 24.6, 25.4, 30.0, 49 and 95.6.

Measurements. Taken from four specimens from samples MW 24.6, 49 and 95.6. L 138–163 (Av. 147.3); Lc 88.5–96 (Av. 92.4); Ln 45–68 (Av. 53.6); Dmax 63–68 (Av. 65.5); Dn 26–30 (Av. 27.6); Lsp 9–12 (Av. 10.4); Ln/L 0.3–0.42; L/Dmax 2.2–3.0.

Remarks. The vesicle surface has a small number of irregularly scattered, robust spines. These are predominantly simple but are interspersed with rare bifurcate, multifurcate and lambda-shaped spines. This ornamentation is close to that described by Eisenack (1964) and Laufeld (1974) for *A. crassispina.*

The main difference between *A.* aff. *A. crassispina* and *A. crassispina* lies in the much smaller size of the former and its proportionally shorter neck (i.e. less than half the total length of the vesicle). This comparison is true also for the specimens of *A.* cf. *A. crassispina* described from Poland by Wrona (1980).

Specimens of *A.* aff. *A. crassispina* from Martins Well are larger than those from the Garra Limestone and the ornamentation is denser.

Angochitina dimorpha Taugourdeau & Jekhowsky, 1960

Fig. 10F, G

Angochitina dimorpha Taugourdeau & Jekhowsky 1960: 1221, pl. 3, figs 38–40.

Material. Eighty-seven specimens from samples MW 15.0, 18.6, 24.6, 25.4, 34.0, 39.9, 49 and 95.6.

Measurements. Taken from nine specimens from samples MW 18.6, 24.6, 25.4, 39.9, 49 and 95.6. L 117–144 (Av. 128); Lc 70–105 (Av. 88.6); Ln 28–52

Fig. 10. A–C, *Angochitina comosa* Taugourdeau & Jekhowsky. A, B, QMF 25470, × 350, and enlargement of neck and collarette × 900, MW 25.4. C, QMF 25471, × 300, MW 18.6. D, E, *Angochitina* cf. *A. callawayensis* Urban & Kline, QMF 25472, × 350, and enlargement of vesicle wall showing spine form × 1500, MW 24.6. F, G, *Angochitina dimorpha* Taugourdeau & Jekhowsky, a form with no collar QMF 25473, enlargement of neck × 1100, and × 350, MW 24.6. H, *Angochitina* sp. C, QMF 25474, × 350, MW 34.2.1, *Angochitina hypenetes* Winchester-Seeto, QMF 25475, × 350, MW 39.9.

(Av. 39.3); Dmax 57–65 (Av. 60.6); Dn 23–32 (Av. 28.1); Lsp 3–7 (Av. 4.8); Ln/L 0.2–0.42; L/Dmax 1.9–2.4; Dn/Dmax 0.38–0.5.

Description. A. dimorpha is a relatively small species of *Angochitina* with an oval, club-shaped to subcylindrical chamber. The maximum diameter is in the lower third of the vesicle but rarely at the basal edge. Flexure is gentle and generally indistinct, leading to a short, cylindrical neck; some individuals have a short, slightly flared collar. The base is strongly convex and the aboral margin is broadly rounded.

Short, robust thorn-like spines cover the entire vesicle surface; many spines are curved. The ornamentation is relatively sparse (3–4 spines per 100 μm²).

Remarks. Taugourdeau & Jekhowsky (1960) stressed an apparent difference between forms with a collar (e.g. their fig. 38) and those without (their figs 39, 40), hence the name *dimorpha*. This distinction is observed in specimens from Martins Well, but a number of intermediate forms suggest that the disparity is not as marked as that suggested by Taugourdeau & Jekhowsky.

In other respects, such as spine form and distribution, the two populations from the Sahara and Australia are very similar.

Angochitina hypenetes Winchester-Seeto, 1993

Fig. 10I

Angochitina hypenetes Winchester-Seeto 1993: fig. 7.1–7.5.

Material. A single specimen from sample MW 39.9.

Measurements. L 147; Lc 96; Ln 51; Dmax 58.5; Dn 25; Lsp 5.6; Ln/L 0.35.

Remarks. Surface ornamentation is largely obscured by an organic coating, so spine density is difficult to establish; all other features, however, are consistent with *A. hypenetes* from the Garra Limestone (Winchester-Seeto 1993).

Angochitina sp. A

Fig. 9F

Angochitina sp. B.—Winchester-Seeto 1993: fig. 7.10–7.15.

Material. Seven specimens from samples MW 18.6, 24.6, 25.4 and 49.

Measurements. Taken from all seven specimens. L 125–147 (Av. 139.7); Lc 78–99 (Av. 91); Ln 43–54.4 (Av. 48.6); Dmax 46–68 (Av. 53.3); Dn 24–34.4 (Av. 28.6); Lsp 4–8 (Av. 5.9); Ln/L 0.31–0.41; L/Dmax 2.1–3.1.

Remarks. The present occurrence extends the range of the species into Assemblage 2 from the Garra Limestone (Winchester-Seeto 1993).

Angochitina sp. B

Fig. 7A–E

Material. One hundred and one specimens from samples MW 13.7, 18.6?, 20.9, 24.6, 25.4, 30.0, 39.9, 49 and 51.

Measurements. Taken from 15 specimens from samples MW 18.6, 24.6, 25.4, 39.9 and 49. L 114–163 (Av. 126.8); Lc 66–96.2 (Av. 80.3); Ln 30–72 (Av. 55); Dmax 43–71.4 (Av. 58.2); Dn 18–30 (Av. 23.7); Dcoll 24–42 (Av. 33); Lsp 2.5–11.0 (Av. 7.2); Ln/L 0.26–0.52; L/Dmax 1.9–3.2; Dmax/Dn 2.1–3.0. Note that Ln/L varies considerably because of difficulties in determining the boundary of the neck and the chamber due to the very elongate flexure.

Description. A species of *Angochitina* with an ovoid to pyriform chamber and an elongate flexure leading to a relatively short neck. The neck is surmounted by a wide collar that is greatly expanded at the aperture (Dn/Dcoll = 0.5–0.88).

The vesicle has a sparse scattering of spines, generally very fine on the collar and neck, becoming more robust on the chamber. Rare bifurcate spines may be present on the neck, but those on the chamber consist predominantly of simple, broad-based spines with an almost triangular shape, giving a thorn-like aspect. Near the basal edge many of the spines take on a node-like appearance.

Remarks. The characteristic node-like appearance of the spines near the basal edge may be partly due to spine breakage and secondary infilling. Better preserved specimens are required for confirmation, so this species has been kept in open nomenclature.

A. comosa has a similar guise but differs in having a more spheroid chamber, a highly convex base, a rounded basal edge and a slightly narrower aperture (see Fig. 11 relating total length to the ratio Dmax/Dn.) The ornamentation of *A. comosa* is much denser and consists of many bifurcate spines on the chamber, with no evidence of 'nodes' or triangular spines near the basal edge.

Many individuals of *Sphaerochitina sphaerocephala* (Eisenack) resemble *Angochitina* sp. B in shape (e.g. Eisenack 1955, pl. 1, figs 5, 6), but no spinose ornamentation has been reported in the former species.
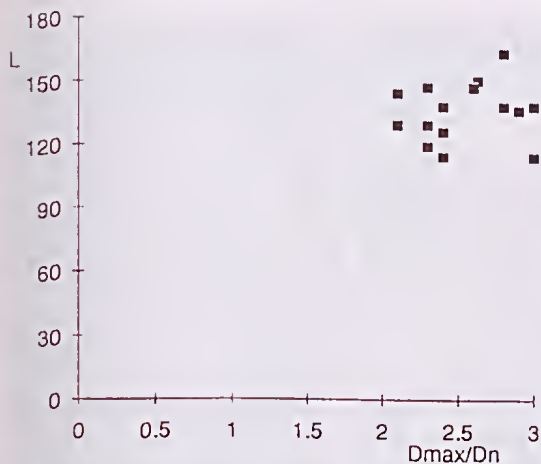
Fig. 11. Intraspecific variation in *Angochitina* sp. B; L = length of vesicle, Dmax/Dn = maximum diameter of vesicle/diameter of neck.

Angochitina sp. C

Fig. 10H

Material. Thirty-five specimens from samples MW 25.4, 34 and 34.2.

Measurements. Taken from five specimens from samples MW 25.4 and 34.2. L 129–146 (Av. 138.8); Lc 69–84 (Av. 80.7); Ln 45–75 (Av. 58.1); Dmax 48–60 (Av. 52.8); Dn 22.5–30 (Av. 26.1); Lsp 2.5–5 (Av. 3.3); Ln/L 0.35–0.52; L/Dmax 2.1–3.0; Dn/Dmax 0.37–0.59.

Description. A species of *Angochitina* with a chamber that varies from spheroidal to a slender oval shape. The basal edge is broadly rounded and the base is convex. Flexure is indistinct; the chamber tapers gently to a quite narrow, nearly cylindrical neck with a very slight flare at the aperture. The neck occupies one-third to one-half the total length. Short, fine spines, ranging from simple to bifurcate in form, cover all of the vesicle, except the edge of the collar.

Remarks. The highly variable vesicle shape matches the range depicted by Eisenack for *Sphaerochitina sphaerocephala*, especially those specimens designated as intermediate between *S. sphaerocephala* and *S. acanthifera* (Eisenack 1972b, pl. 28, figs 21, 22). Eisenack (1964) referred without accompanying illustrations to a similar complex from Gotland.

The existence of very fine spines on *Angochitina* sp. C rules out assignment to *S. sphaerocephala* which is generally smooth or possesses only tubercles (Eisenack 1932). *S. acanthifera*

has short spines, but its characteristic 'bend' at the maximum diameter of the chamber is found in only a few specimens of *Angochitina* sp. C. The Queensland material has been placed in *Angochitina* because of the presence of sparsely distributed spines as opposed to tubercles or dense erect spines as found on *Sphaerochitina* (Eisenack 1955).

Angochitina hypenetes also resembles this species but has shorter, finer spines more sparsely distributed on the vesicle, and lacks evidence of a distinct collar.

Angochitina sp. D

Fig. 12F, G

Material. One partially flattened specimen from sample BOO 28.

Measurements. L 107; Lc 39; Ln 68; Dmax 65; Dn 20; Lsp 12; Ln/L 0.36; L/Dmax 2.35.

Description. This small specimen has been badly distorted by flattening. The chamber has an almost square aspect, with a flat base but a rounded basal edge. Flexure is ill-defined, leading to a short neck that narrows slightly towards the aperture. There is a small collar with a crenulate edge.

The spinose ornamentation is distinctive but its distribution is difficult to determine due to poor preservation leaving few spines on the chamber. The neck spines are substantial and relatively thick, ranging in form from simple to bifurcate. The bifurcate spines may be broad-based as a result of the coalescence of two spines or may be raised slightly from the vesicle surface by a short stalk.

Remarks. It is possible that this species belongs to *Gotlandochitina* but the presence of a linear arrangement of spines on the chamber cannot be confirmed in this single specimen. The peculiar ornamentation distinguishes the species from any other of similar size or shape.
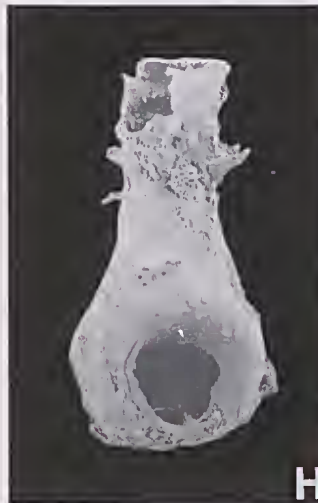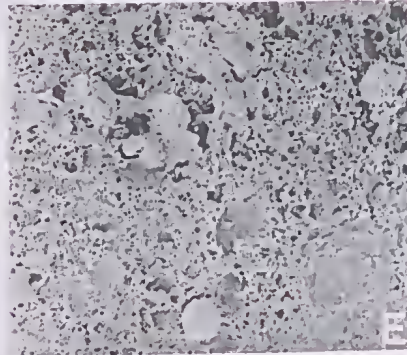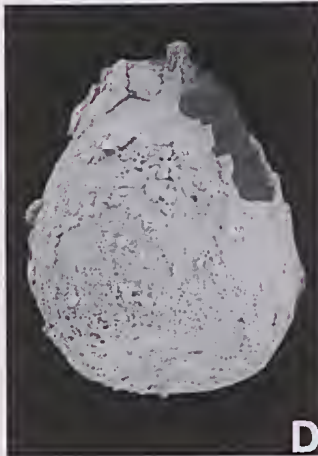
Angochitina sp. E

Fig. 9I

Material. One specimen from sample MW 39.9.

Measurements. L 219; Lc 86; Ln 133.3; Dmax 64.5; Dn 30; Ln/L 0.6.

Description. This species has a narrow, chevron-shaped chamber with a convex base and no apparent basal edge. An indistinct flexure leads to a relatively long neck occupying more than half of the total vesicle length. The neck is subcylindri-

cal in form but exhibits variable width along its length due to flattening and twisting; this feature may be teratological in nature. A small collar may be present, flaring slightly towards the aperture.

Spinose ornamentation on the vesicle consists of relatively short spines that may be simple or lambda-shaped. Spines are reduced in length and number on the neck, with very few appearing on the upper part of the neck.

Remarks. This single individual may be merely an aberrant form of *A.* aff. *A. crassispina*, as suggested by the presence of a number of lambda-shaped spines.

Angochitina sp. E also exhibits many similarities to *A. longicolla*, described from the Baltic Silurian by Eisenack (1959). The general shape, size and proportions of *A. longicolla* match those of the Australian specimen (e.g. the proportion L/Dmax is 3.2–3.5 in the specimens figured by Eisenack and is 3.4 in the Australian specimen). This similarity is reinforced by the presence of lambda-shaped spines on both groups. The only differences are the reduced number of spines and the slightly longer neck of the Australian specimen; Ln/L is 0.6 in the Martins Well specimen, whereas in the specimens figured by Eisenack (1959, pl. 2, figs 8, 9) Ln/L ranges from 0.47 to 0.5.

This species is also similar in shape to *Angochitina* sp. 2 of Paris (1976) and to *A.* cf. *A. longicollis* described by Wrona (1980), but, as neither Paris nor Wrona figured specimens with well-preserved ornamentation, the similarities are difficult to substantiate.

Genus **Bulbochitina** Paris, 1981a

Type species. Bulbochitina bulbosa Paris, 1981a.

Bulbochitina bulbosa Paris, 1981a

Fig. 12A–E

Bulbochitina bulbosa Paris 1981a: 134–135, pl. 35, figs 1–8, 10–19, pl. 37, fig. 1.

Material. Twenty-five specimens from samples BOO 13.1 and BOO 17.8.

Measurements. Taken from eleven specimens from sample BOO 13.1. L 111–158 (Av. 128.8); Dmax 107–165 (Av. 128.5); Da 41–80 (Av. 57.5); L/Dmax 0.79–

1.4; Da/Dmax 33–50%. See Fig. 13 for a graph relating total length of the vesicle (L) to maximum diameter of the vesicle (Dmax).

Remarks. One specimen (Fig. 12B) has what appears to be the remnant of a basal carina, but no other individual of this population displays this character. In general the basal margin of most specimens of *Bu. bulbosa* from Boola Quarry is well rounded. The presence of a carina, which distinguishes the genus *Armoricochitina*, is very difficult to observe if the feature has been eroded, but generally the aboral margin of *Armoricochitina* is relatively sharp and more abrupt than is observed on the specimens from Boola Quarry.
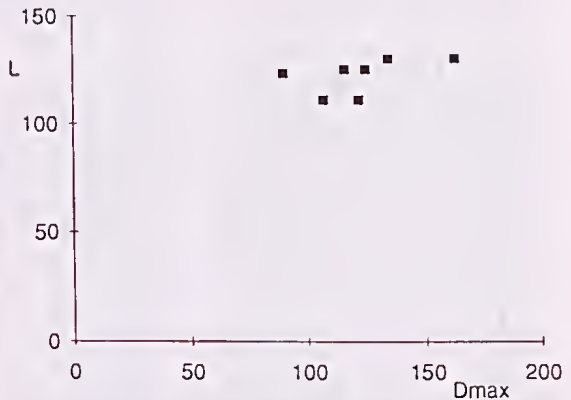

Fig. 13. Intraspecific variation in *Bulbochitina bulbosa* Paris, 1981a; L = length of vesicle, Dmax = maximum diameter of vesicle.

Genus **Bursachitina** Taugourdeau, 1966

Type species. Desmochitina bursa Taugourdeau & Jekhowsky, 1960.

Bursachitina mawsonae Winchester-Seeto, 1993

Fig. 81

Bursachitina mawsonae Winchester-Seeto 1993: 748, fig. 9.1–9.8.

Material. Twelve specimens from samples MW 20.9, 49, 69, 74, 78.6 and 95.6.

Measurements. Taken from two specimens from samples MW 49 and MW 95.6. L 142.8–155; Dmax 85–92; Da 63–71.5; Da/Dmax 74–77%.

Fig. 12. A–E, *Bulbochitina bulbosa* Paris, BOO 13.1. A, NMV P137603, × 300. B, NMV P137604, × 300. C, NMV P137605, × 300. D, E, NMV P137606, × 300, and enlargement of chamber wall showing ornamentation, × 1000. F, G, *Angochitina* sp. D, small, partially flattened specimen NMV P137607, × 400, and enlargement of neck showing detail of neck spines, × 1400, BOO 28. H, *Gotlandochitina* sp. B, NMV P137608, × 350, BOO 17.8. I, *Bursachitina* sp., NMV P137609, × 300, BOO 13.1.

Remarks. The vesicle shapes of *Desmochitina parkerae* Urban and *B. mawsonae* are superficially quite similar. The material from Martins Well contains slightly larger specimens of *B. mawsonae* than those from the Garra Limestone, placing them in the size range of *D. parkerae*. The diameter of the oral opening, however, serves to differentiate the two taxa; the aperture of the Martins Well specimens is approximately 75% of the maximum diameter of the vesicle, much less than 80–90% found in *D. parkerae*.

The specimen in Fig. 8I represents one extreme of intraspecific variation, where the maximum diameter is only 55% of the total length of the vesicle. This feature is common to individuals of this species from Martins Well and fits within the range of shapes from the type locality in the Garra Limestone. More typical members of *Bursachitina* have a maximum diameter closer to that of the length of the vesicle, but the amended diagnosis given by Paris (1981a: 137) does not exclude the forms observed from Martins Well.

Bursachitina sp.

Fig. 121

Material. Five specimens from sample BOO 13.1.

Measurements. Taken from two specimens. L 140.5–153.5; Dmax 115–118; Da 53–55.5; L/Dmax 1.2–1.4; Da/Dmax 0.46–0.47.

Description. This species has a conical to ovoid vesicle, with weak to moderately convex flanks. Maximum diameter occurs in the lower half to lower third of the length of the vesicle, but not at the aboral margin. The aperture is quite narrow, less than 50% of the maximum diameter, and is surrounded by a short collar with a crenulate edge. The broadly rounded basal edge leads to a flat or concave base, displaying a large basal callus. Ornamentation is poorly preserved but appears to be felt-like, with no evidence of spines.

Remarks. The general appearance of this species is reminiscent of *Bursachitina maritima* (Paris), especially the broadly rounded aboral margin

and the basal scar. Ornamentation also appears to be similar, despite the poor preservation of the specimens from Boola Quarry. The vesicle shape differs in being somewhat narrower than that of *B. maritima*, thus giving a much larger apical angle (i.e. approximately 45°). The aperture is also smaller, being only 46–47% of the maximum diameter, whereas *B. maritima* has an aperture up to 54–57% of the maximum diameter. The paucity of specimens makes a conclusive identification difficult, as these may merely represent extremes of intraspecific variation.

Grignani (1967, pl. 1, fig. 27) figured a specimen, assigned to *Desmochitina urna* Eisenack, with a similar shape to the individuals from Boola. This specimen, from the Siegenian of Tunisia, may be related to the Boola group.

Despite the similarity of the outline of this species to *Armoricochitina ceneratiensis* (Paris), there is no evidence of a carina at the basal margin, thus excluding the species from *Armoricochitina*.

Genus Gotlandochitina Laufeld, 1974

Type species. Gotlandochitina martinssoni Laufeld, 1974.

Gotlandochitina implicationis (Urban, 1972)

Fig. 14A, B

Angochitina implicationis Urban 1972: 15, pl. 3, figs 1–7.—Urban & Newport 1973: pl. 1, figs 7, 8.—Winchester-Seeto 1993: 746, figs 7.6, 7.7.

*Material.* One specimen from sample MW 34.2

Measurements. L 114; Le 69; Ln 45; Dmax 60; Dn 24; Lsp 3.5.

Remarks. The specimen from Martins Well is smaller than those from the United States or New South Wales and has a longer, better defined neck, but clearly displays the linear arrangement of spines described by Urban (1972).

Gotlandochitina kutjala n. sp.

Fig. 8A–D

Fig. 14. A, B, *Gotlandochitina implicationis* (Urban), QMF 25487, × 350, and enlargement of lower part of chamber showing linear arrangement of ornamentation × 1200, MW 34.2. C, D, *Gotlandochitina* cf. *G. marettensis* Paris, QMF 25488, × 350, and enlargement of lower part of chamber showing details of ornamentation × 600, MW 49. E–G, *Gotlandochitina marettensis* Paris. E, F, QMF 25489, × 350, and enlargement of chamber wall showing ornamentation and 'holes' that may indicate the presence of parasites × 900, MW 25.4. G, QMF 25490, × 350, MW 24.6. H, I, *Gotlandochitina* aff. *G. philipotti* (Paris), QMF 25491, enlargement of chamber wall × 650, and × 350, MW 39.9.
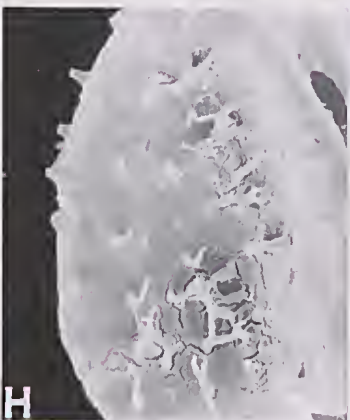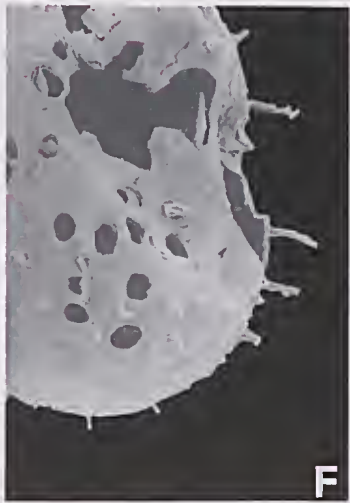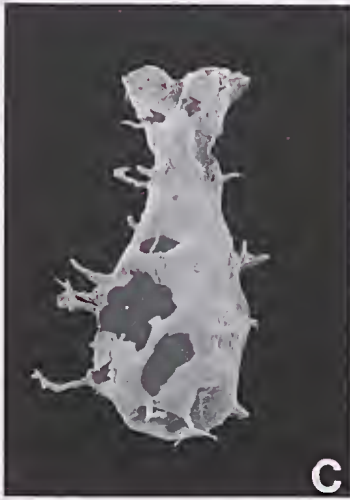
Etymology. Named for the Kutjala, one of the Aboriginal tribes of the Broken River area.

Holotype. QMF 25492, Fig. 8A, D.

Type horizon and locality. MW 18.6, MW section of the Shield Creek Formation, Broken River area of Queensland.

Paratypes. QMF 25493, Fig. 8B, C; QMF 25494, Fig. 8E.

Other material. One hundred and eighteen specimens from samples MW 18.6, 22.6, 24.6, 25.4, 39.9, 49 and 78.6. The specimens are poorly preserved, none having the ornamentation intact.

Measurements. Taken from twenty-one specimens from samples MW 18.6, 24.6, 25.4, 39.9 and 49. L 88–177 (Av. 147.8, holotype 163); Lc 62–119 (Av. 94, holotype 102); Ln 25–69 (Av. 53.3, holotype 61); Dmax 44–68 (Av. 59.6, holotype 65); Dn 15.5–44 (Av. 27.5, holotype 34); Lsp 2–9.3 (Av. 5.4, holotype 7); Ln/L 0.3–0.45 (holotype 0.37); L/Dmax 2.0–3.1 (holotype 2.5).

Diagnosis. Chamber slender, elongate and club-shaped; flexure conspicuous; neck short with collar expanded at aperture. Spines short, distinct, in subparallel vertical rows.

Description. The slender, elongate, claviform vesicle has a conspicuous flexure without shoulders. The neck comprises less than half the length of the vesicle and has a clearly defined, slightly flared collar with a crenulate edge. The base is strongly convex. The shape of the chamber varies considerably, and this is further complicated by the distortional effects of compression on different parts of the chamber. The maximum diameter of the vesicle appears between the lower half to the lower third of the chamber length, so that the form of the chamber ranges from a tear-drop to a club-shape.

Ornamentation consists of short spines distributed relatively sparsely (3–5 per $100\mu m^2$) in sub-parallel, vertical rows covering the collar, neck, chamber and base. The length of the spines is reduced on the collar. Though predominately simple in form, the spines may also be bifurcate or multifurcate. Curvature is common among the simple spines.

Remarks. In shape and dimensions, *G. kutjala* closely matches the specimens depicted by Urban (1972) as *Angochitina capillata* Eisenack, and by Lange (1967) and Winchester-Sceto (1993) as *A.* cf. *A. capillata* Eisenack. The differences lie in the sparser ornamentation of *G. kutjala* and in the relatively finer spines.
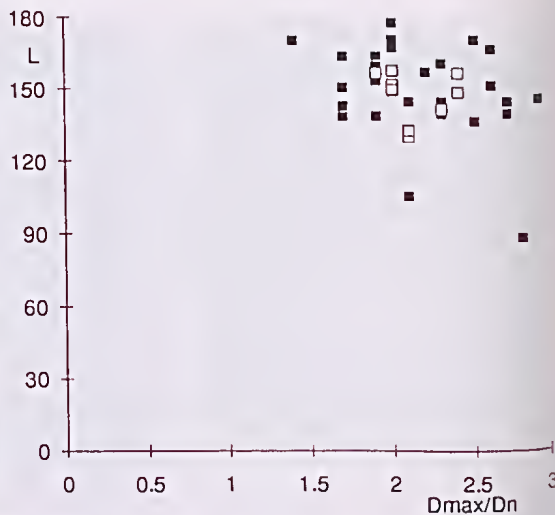
The ornamentation of *G. kutjala* resembles

Fig. 15. Intraspecific variation in *Gotlandochitina kutjala* n. sp. (black squares) and *G. marettensis* Paris. 1981b (white squares); L = length of vesicle. Dmax/Dn = maximum diameter of vesicle/diameter of neck.

that of *Angochitina filosa* Eisenack as illustrated by Wrona (1980), but the former may be distinguished by its shorter neck. *Angochitina echinata* Eisenack (see Eisenack 1931, 1972a; Laufeld 1974; Wrona 1980) may also be confused with *G. kutjala*, but *A. echinata* has a more spherical chamber quite unlike that of *G. kutjala*.

In each of the above examples of similar species, the illustrations and descriptions give no indication of a linear arrangement of the spines. *Gotlandochitina marettensis* Paris is probably the closest species in this regard, but it differs from *G. kutjala* in having longer, more complex spines and a more spherical chamber with the maximum diameter approximately halfway down the length of the chamber. Fig. 15 illustrates the close similarity between *G. kutjala* and *G. marettensis* in a graph of the total length (L) versus maximum diameter of chamber/diameter of neck (Dmax/Dn).

Gotlandochitina marettensis Paris, 1981b

Fig. 14E–G

? *Angochitina bifurcata* Collinson & Schwalb 1955: 21–22, pl. 2, figs 1–3.—Costa 1967: 97, pl. 1, fig. 9.—Costa 1971: 224, fig. 14.

? *Angochitina* sp.—Paris 1977: 122, pl. 6-16, fig. 14. *Gotlandochitina* cf. *G. bifurcata.*—Paris 1978: pl. 1, fig. 7.

Gotlandochitina marettensis Paris 1981b: 63–65, pl. 5, figs 1, 2, 5, 9, 10.—Paris 1981a: 265, pl. 36, figs 3, 4, 16.

Material. Fifty-four specimens from samples MW 20.9, 22.6, 24.6, 25.4, 30, 39.9 and 49.

Measurements. Taken from nine specimens from samples MW 24.6, 25.4, 39.9 and 49. L 129.5–157 (Av. 146.6); Lc 78–108 (Av. 94.3); Ln 45–64 (Av. 52.0); Dmax 48–70 (Av. 62.6); Dn 18–34 (Av 28.1); Lsp 2–10.2 (Av. 7.2); Ln/L 0.3–0.41; L/Dmax 2.2–3.1.

Remarks. The shape and dimensions of the specimens from Martins Well closely match those from France (Paris 1981b). Poor preservation of ornamentation makes determination of maximum spine length difficult and assessment of the presence of rows of spines (as opposed to irregularly scattered spines) impossible. Spinose ornamentation consists predominantly of simple and bifurcate spines, but the apparent lack of multifurcate spines may also be related to preservation. Poor preservation may also explain the much shorter spines found on the Australian specimens (i.e. less than half the average length of the spines in the French specimens). It is also possible that the shorter spines represent a regional variation of the species.

Paris (1981b) noted the similarities between *G. marettensis* and *Angochitina bifurcata* Collinson & Schwalb from North and South America. Minor differences in *G. marettensis* include the presence of simple spines amongst the bifurcate ones and a slightly larger vesicle. It is not possible to judge from the illustrations provided by Collinson & Schwalb (1955) or Costa (1971) whether the spines on *A. bifurcata* are arranged in rows. Thus, the relationship between *A. bifurcata* and *G. marettensis* cannot yet be resolved. However, the similarities are so striking that if the two species are not conspecific, then there must be some evolutionary connection.

This is the first report of *G. marettensis* from the Pragian; however, *A. bifurcata* is known from the Lochkovian.

Gotlandochitina cf. G. marettensis? Paris, 1981b

Fig. 14C, D

?*G.* cf. *G. marettensis.*—Paris 1979: 353, fig. 1 (*nomen nudum*).—Paris 1981b: 65, pl. 5, figs 12, 15.

Material. Three specimens from sample MW 49.

Measurements. Taken from two of the specimens. L 141; Lc 84–90; Ln 51–57; Dmax 48–57; Dn 19–27; Lsp 15–24; Ln/L 0.36–0.4; L/Dmax 2.5–2.9.

Remarks. The shape, dimensions and ornamentation of these specimens are almost identical with *G.* cf. *G. marettensis* of Paris, except for a coronet of spines at the aperture on specimens from Martins Well. *G.* cf. *G. marettensis* may be merely an extreme variant of *G. marettensis*, a suggestion supported by the fact that the two forms are present at both Martins Well and Le Lezais, Gahard. This is the first report of this species from the Pragian.

Gotlandochitina aff. G. philipotti (Paris, 1976)

Fig. 14H, I

Material. Twenty-two specimens from samples MW 18.6, 30, and 39.9.

Measurements. Taken from four specimens from MW 18.6 and 39.9. L 129–139 (Av. 135); Lc 81–90 (Av. 87); Ln 48–69 (Av. 53.5); Dmax 60–63.8 (Av. 61.2); Dn 24–33 (Av. 29); Lsp 3.2–9 (Av. 6.9); Ln/L 0.35–0.37; L/Dmax 2.2–2.3; apical angle 47°–57°.

Description. Chamber shape varies from spheroid to ovoid, with a well rounded basal edge and a weak to strongly convex base. This is topped with a relatively short, cylindrical neck and may have a collar expanded at the aperture. The flexure is elongate, and shoulders are present but weak.

Fine, short spines cover the neck and collar. The ornamentation on the chamber consists of strong spines, ordered in rows, stretching from the basal edge to the base of the neck. The spines are most obvious at the middle of the chamber and tend to be shorter and less dense near the basal edge. Spines may be simple but are more commonly bifurcate or multifurcate with wide or coalesced bases; they are frequently tangled at the distal end.

Remarks. The specimens from Martins Well have a very similar spine form to that illustrated for *G. philipotti* by Chlupáč et al. (1985, pl. 3, figs 11, 12), and also conform very closely to the description and dimensions given by Paris (1976). Differences lie in the distribution and size of the ornamentation. Fine, short spines are found on the neck of specimens from Martins Well, contrasting with the fairly robust spines of European specimens, and there is no evidence of a gap in ornamentation between the spines on the neck and those on the chamber, a distinctive feature of *G. philipotti*.

Gotlandochitina sp. A

Fig. 8F, G

Material. Nine specimens from samples MW 24.6, 25.4? and 39.9.

Measurements. Taken from three specimens from samples MW 24.6, 25.4? and 39.9. L 120–167 (Av. 141.6); Lc 75–92 (Av. 84.6); Ln 44–75 (Av. 56.7); Dmax 52–65 (Av. 58); Dn 23–34 (Av. 29); Ln/L 0.37–0.45; L/Dmax 2.3–2.6.

Description. This species has an ovoid–cylindrical vesicle with a long, slender chamber, a convex base and no obvious basal edge. The neck is cylindrical to subcylindrical and occupies one-third to one-half of the total length of the vesicle.

Spines occur in a number of rows on the chamber, possibly extending onto the base (poor preservation makes this observation equivocal). The few spines left intact range from rare, simple spines, to more common bifurcate spines in antler shapes, to bifurcate spines with broad bases. Ornamentation occurs on all parts of the neck including the collar, and is generally smaller and sparser than that on the chamber.

Remarks. The shape of *Gotlandochitina* sp. A is difficult to determine as all of the specimens show some degree of distortion and breakage. There are a number of similarities in ornamentation with *Gotlandochitina villosa* Laufeld. Both the long branched spines near the aboral part of the chamber and the broad-based bifurcate spines figured by Laufeld (1974, fig. 56C, D) are also present in some individuals from Queensland. In addition, Laufeld's observation that the spines on the aboral part of the chamber tend to curve towards the oral part of the vesicle also applies to *Gotlandochitina* sp. A. The species from Queensland, however, has a denser ornamentation covering all of the neck including the collar.

Gotlandochitina sp. B

Fig. 12H

Gotlandochitina sp. C.—Winchester-Seeto 1993: 754, fig. 10.3.

Material. Three specimens from samples BOO 17.8 and 28.

Measurements. Taken from two specimens from BOO 17.8 and 28. L 123–160; Lc 66–95; Ln 57–65; Dmax 57–82; Dn 27–37; Lsp 9–17; L/Ln 2.2–2.5; Dmax/Dn 2.1–2.2.

Remarks. The three individuals from Boola Quarry differ only slightly from those found in the Garra Limestone (Winchester-Seeto 1993). A small number of thick, simple and bifurcate spines dominate the vesicle. The ornamentation is slightly longer on specimens from Boola Quarry, and between the large spines a number of small, very fine spines occur. One individual shows evidence of a row of thick spines encircling the neck.

Gotlandochitina sp. B can be differentiated from *Angochitina caeciliae* Paris by its generally longer vesicle and by the predominantly straight, simple spines, as opposed to the curved spines in *A. caeciliae.*

ACKNOWLEDGEMENTS

REFERENCES

BAYER, U. & McGHEE, G. R., 1989. Periodicity of Devonian sedimentary and biological pertubations: implications for the Devonian timescale. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 1989: 1–16.

CHLUPÁČ, I., LUKES, P., PARIS, F. & SCHÖNLAUB, H. P., 1985. The Lochkovian–Pragian boundary in the Lower Devonian of the Barrandian area (Czechoslovakia). *Jahrbuch der Geologischen Bundesanstalt* 128: 9–41.

COLLINSON, C., & SCHWALB, H., 1955. North American Paleozoic Chitinozoa. *State Geological Survey, Urbana, Report of Investigations* 186: 1–33.

COSTA, N. M., 1967. Quitinozoários Silurianos e Devonianos da Bacia Amazônica e sua correlaçao estratigráifea. *Atas do Simpósio sobre a Biota Amazônica* 1: 87–119.

COSTA, N. M., 1971. Quitinozoários Brasileiros e sua importancia estratigráfica. *Anais Acadamia Brasil Ciencias* 43: 209–272.

DIEZ, M. D. C. R. & CRAMER, F. H., 1978. Iberian chitinozoans. 2. Lower Devonian forms (La Vid Shales and equivalents). *Palinologia extraordinario* 1: 203–217.

DUNN, D. L., 1959. Devonian chitinozoans from the Cedar Valley Formation in Iowa. *Journal of Paleontology* 33: 1001–1017.

EISENACK, A., 1931. Neue Mikrofossilien des baltischen Silurs 1. *Paläontologische Zeitschrift* 13: 74–118.

EISENACK, A., 1932. Neue Mikrofossilien des baltischen Silurs 2. (Foraminiferen, Hydrozoen, Chitinozoen u.a.). *Paläontologische Zeitschrift* 14: 257–277.

EISENACK, A., 1955. Neue Chitinozoen aus dem Silur des Baltikums und dem Devon der Eifel. *Senckenbergiana lethaea* 36: 157–188.

EISENACK, A., 1959. Neotypen baltischer Silur-Chitinozoen und neue Arten. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 108: 1–20.

EISENACK, A., 1964. Mikrofossilien aus dem Silur Gotlands. Chitinozoen. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 120: 308–342.

EISENACK, A., 1968. Über Chitinozoen des Baltischen Gebietes. *Palaeontographica, Abteilung A* 131: 137–198.

EISENACK, A., 1972a. Chitinozoen und anderen Mikrofossilien aus der Bohrung Leba, Pommern. *Palaeontographica, Abteilung A* 139: 64–87.

EISENACK, A., 1972b. Beiträge zur Chitinozoen-Forschung. *Palaeontographica, Abteilung A* 140: 117–130.

GAO LIAN-DA, 1986. Chitinozoans. In *Devonian Stratigraphy, Palaeontology and Sedimentary Facies of Longmenshan, Sichau*, Hou Hong-fei, ed., Chengdu Institute of Geology and Mineral Resources and Institute of Geology, Chinese Academy of Geological Sciences, Chengdu, 356–357.

GRIGNANI, D., 1967. Correlation with Chitinozoa in the Devonian and Silurian in some Tunisian well samples. *Review of Palaeobotany and Palynology* 5: 315–325.

JAGLIN, J. C., 1986. Nouvelles espéces de Chitinozoaires du Pridoli de Libye. *Revue de Micropaléontologie* 29 (1): 44–54.

JARDINÉ, S. & YAPAUDJIAN, L., 1968. Lithostratigraphie et palynologie du Dévonien–Gothlandien gréseux du Bassin de Polignac (Sahara). *Revue de l'Institut Français du Pétrole* 23: 439–455.

JELL, J. S., 1968. New Devonian rock units of the Broken River Embayment, north Queensland. *Proceedings of the Royal Society of Queensland* 87: 63–76.

KENNEY, J. P. L., 1937. Tyers River limestone. *Records of the Geological Survey of Victoria* 1936: 702–707.

LANGE, F. W., 1967. Biostratigraphie subdivision and correlation of the Devonian in the Paranà Basin. *Boletim Paranaense de Geociências* 21/22: 63–98.

LAUFELD, S., 1974. Silurian Chitinozoa from Gotland. *Fossils and Strata* 5: 1–130.

MAGLOIRE, L., 1967. Étude stratigraphique, par la palynologie, des dépôts argilo-gréseux du Silurien et du Dévonien inférieur dans la région du Grand Erg occidental (Sahara algérien). In *International Symposium on the Devonian System, Calgary, 1967*, vol. 2, D. H. Oswald, ed., Alberta Society of Petroleum Geologists, Calgary, 473–491.

MASSA, D., & MOREAU-BENOIT, A., 1976. Essai de synthèse stratigraphique et palynologique du système Dévonien en Libye occidentale. *Revue de l'Institut Français du Pétrole* 31: 287–333.

MAWSON, R. & TALENT, J. A., in press. Age of an Early Devonian carbonate fan and isolated limestone clasts and megaclasts, east-central Victoria. *Proceedings of the Royal Society of Victoria* 106.

MAWSON, R., TALENT, J. A., BEAR, V. C., BENSON, D. S., BROCK, G. A., FARRELL, J. R., HYLAND, K. A., PYEMONT, B. D., SLOAN, T. R., SORENTINO, L., STEWART, M. J., TROTTER, J. A., WILSON G. A. & SIMPSON, A. G., 1988. Conodont data in relation to resolution of stage and zonal boundaries for the Devonian of Australia. *Canadian Society of Petroleum Geologists Memoir* 16: 1–40.

MAWSON, R., TALENT, J. A., BROCK, G. A. & ENGELBRETSON, M. J., 1992. Conodont data in relation to sequences about the Pragian–Emsian boundary (Early Devonian) in south-eastern Australia. *Proceedings of the Royal Society of Victoria* 104: 23–56.

PARIS, F., 1976. Les chitinozoaires. *Mémoires de la Société Géologique et Minéralogique de Bretagne* 19: 93–133.

PARIS, F., 1977. Les chitinozoaires. In *Stratigraphie et Paléogeographie. Précambrien. Ère Paléozoïque*, C. Pomerol & C. Babin, eds, Doin éditeur, Paris, 121–122.

PARIS, F., 1978. Apports du microscope électronique á balayage dans l'étude des chitinozoaires opaques. *Annales des Mines de Belgique* 1978: 193–202.

PARIS, F., 1979. Biostratigraphie des chitinozoaires: un exemple dans l'Emsien supérieur armoricain. In *Septième Réunion Annuelle des Sciences de la Terre—Société géologique de France, Lyon 1979*, 353.

PARIS, F., 1980. Les chitinozoaires. *Mémoires de la Société Géologique et Minéralogique de Bretagne* 23: 52–82.

PARIS, F., 1981a. Les chitinozoaires dans le Paléozoïque du sud-ouest de l'Europe. *Mémoires de la Société Géologique et Minéralogique de Bretagne* 26: 1–412.

PARIS, F., 1981b. Les chitinozoaires. *Mémoires de la Société Géologique et Minéralogique de Bretagne* 24: 47–71.

PHILIP, G. M., 1962. The palaeontology and stratigraphy of the Siluro-Devonian sediments of the Tyers area, Gippsland, Victoria. *Proceedings of the Royal Society of Victoria* 75: 123–246.

PHILIP, G. M., 1965. Lower Devonian conodonts from the Tyers area, Gippsland, Victoria. *Proceedings of the Royal Society of Victoria* 75: 95–117.

PHILIP, G. M. & PEDDER, A. E. H., 1967. The correlation of some Devonian limestones of New South Wales and Victoria. *Geological Magazine* 104: 232–239.

RAHMANI, K., 1978. Présence de chitinozoaires, d'acritarches et de spores dans le Paléozoïque de la région de Rabat, Maroc. *Palinologia extraordinario* 1: 375–384.

REHFISCH, M. W. & WEBB, J. A., 1993. The Early Devonian Coopers Creek Limestone, a redeposited deep-water limestone within the Melbourne Trough, southeastern Australia. *Australian Journal of Earth Sciences* (in press).

SORENTINO, L., 1989. Conodont assemblages spanning the Lochkovian–Pragian (Early Devonian) boundary at Eurimbla, central New South Wales. *Courier Forschungsinstitut Senckenberg* 117: 81–117.

SWEET, W., 1985. Conodonts: those fascinating little whatzits. *Journal of Paleontology* 59: 485–494.

TALENT, J. A., MAWSON, R., ANDREW, A. S., HAMILTON, P. J. & WHITFORD, D. J., in press. Middle Palaeozoic extinction events: quest for isotopic signatures: preliminary data. *Palaeogeography, Palaeoclimatology, Palaeoecology.*

TALENT, J. A. & YOLKIN, E. A., 1987. Transgression-regression patterns for the Devonian of Australia and southern west Siberia. *Courier Forschungsinstitut Senckenberg* 92: 235–249.

TAUGOURDEAU, P., 1966. Les chitinozoaires, techniques d'études, morphologie et classification. *Mémoires de la Société Géologique de France* 45: 1–64.

TAUGOURDEAU, P. & DE JEKHOWSKY, P., 1960. Répartition et description de chitinozoaires Siluro-Dévoniens de quelques sondages de la CREPS, de la CFPA, et de la SN REPAL au Sahara. *Revue de l'Institut Français du Pétrole* 15: 1199–1260.

TELFORD, P. G., 1972. Lower and Middle Devonian conodont faunas from the Broken River Embayment, north Queensland. PhD thesis, Department of Geology and Mineralogy, University of Queensland, Brisbane.

TELFORD, P. G., 1975. Lower and Middle Devonian conodonts from the Broken River Embayment, north Queensland, Australia. *Special Papers in Palaeontology* 15: 1–96.

TYSON, R. V. & PEARSON, T. H., 1991. Modern and ancient continental shelf anoxia: an overview. In *Modern and Ancient Shelf Anoxia*, R. V. Tyson & T. H. Pearson, eds, Geological Society of London Special Publication No. 58, 1–24.

URBAN, J. B., 1972. A reexamination of Chitinozoa from the Cedar Valley Formation of Iowa with observations on their morphology and distribution. *Bulletins of American Paleontology* 63 (275): 1–44.

URBAN, J. B. & KLINE, J. K., 1970. Chitinozoa of the Cedar City Formation, Middle Devonian of Missouri. *Journal of Paleontology* 44: 69–76.

URBAN, J. B. & NEWPORT, R. L., 1973. Chitinozoa of the Wapsipinicon Formation (Middle Devonian) of Iowa. *Micropaleontology* 19: 239–346.

VANDENBERG, A. H. M., 1988. Silurian-Middle Devonian. In *Geology of Victoria*, 2nd edn, J. G. Douglas & J. A. Ferguson, eds, Victorian Division, Geological Society of Australia, Melbourne, 103–146.

VOLKHEIMER, W., MELENDI, D. L. & SALAS, A., 1986. Devonian chitinozoans from northwestern Argentina. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 173: 229–251.

WILSON, G. A., 1989. Documentation of conodont assemblages across the Lochkovian–Pragian (Early Devonian) boundary at Wellington, central New South Wales, Australia. *Courier Forschungsinstitut Senckenberg* 117: 117–171.

WINCHESTER-SEETO, T., 1993. Chitinozoa from the Early Devonian (Lochkovian–Pragian) Garra Limestone, central New South Wales, Australia. *Journal of Paleontology* 66: 738–758.

WRONA, R., 1980. Upper Silurian–Lower Devonian Chitinozoa from the subsurface of southeastern Poland. *Palaeontologia Polonica* 41: 103–165.

WYATT, D. H. & JELL, J. S., 1980. Devonian and Carboniferous stratigraphy of the northern Tasman Orogenic Zone in the Townsville hinterland, north Queensland. In *The Geology and Geophysics of Northeastern Australia*, R. A. Henderson & P. J. Stephenson, eds, Geological Society of Australia, Queensland Division, Brisbane, 201–228.

ZIEGLER, W. & LANE, H. R., 1987. Cycles in conodont evolution from Devonian to mid-Carboniferous. In *Palaeobiology of Conodonts*, R. J. Aldridge, ed., British Micropalaeontological Society Series, Chichester, 147–163.